

Allometry and Adaptation of Body Proportions and Stature in African Pygmies

BRIAN T. SHEA AND ROBERT C. BAILEY

Departments of Cell and Molecular Biology, and Anthropology, Northwestern University, Chicago, Illinois 60611 (B.T.S.); Department of Anthropology, University of California at Los Angeles, Los Angeles, California 90024 (R.C.B.)

KEY WORDS Ontogenetic scaling, Anthropometrics, Growth physiology, Microevolutionary dwarfism, Tropical forest

ABSTRACT We have analyzed the growth allometry of external body proportions in Efe pygmies from Zaire and combined these data with values from the literature for comparable dimensions in adult pygmies and nonpygmies. We sequentially tested the hypotheses that adult proportion differences between 1) male vs. female Efe, and 2) pygmies vs. nonpygmies result from ontogenetic scaling, or the differential extension of common patterns of growth allometry. Results indicate an almost complete concordance of allometric trajectories for male and female Efe. These preliminary analyses also strongly suggest that adult nonpygmy Africans generally differ from pygmies in their terminal size and correlated allometric consequences, rather than in more fundamental alterations of underlying patterns of growth. Biacromial diameter emerges as the measurement most likely to depart from this general pattern. These results provide further evidence that shifts in systemic growth hormones yielding differences in terminal overall body size may be accompanied by global and coordinated allometric transformations.

Certain proportion differences previously interpreted by some as specific evidence of primitive retention in pygmies in fact reflect simple growth allometric correlates of the derived rapid size decrease in these groups. Selected divergent body proportions characterizing adult pygmies, previously interpreted by some as independent evidence of climatic adaptation, also reflect such allometric correlates of ontogenetic scaling. We critically assess arguments that the small overall body size of pygmies was specifically selected for reasons of thermoregulatory efficiency, and consider an alternative or complementary scenario, based on selection for small size in order to reduce caloric requirements. © 1996 Wiley-Liss, Inc.

The short stature and distinctive body proportions of African pygmies have long been of interest to physical anthropologists studying a range of significant evolutionary issues, including climatic adaptation, rates and degrees of morphological differentiation, and the developmental basis of size alteration. Interest in these theoretical issues has generated numerous detailed anthropometric studies of African pygmies, who lie at the extreme low end of the worldwide dis-

tribution for adult stature and body weight (e.g., Czekanowski, 1922; Gusinde, 1948; Schebesta, 1938, 1952; Ghesquiere and Karvonen, 1981; Hiernaux, 1968, 1977; Vallois and Marquer, 1976; Marquer, 1972; Bako-

Received November 24, 1992; accepted October 7, 1995.

Address reprint requests to Dr. Brian T. Shea, Department of Cell and Molecular Biology, Northwestern University, 303 East Chicago Avenue, Chicago, IL 60611.

nyi, 1976). Continuing interest in the African pygmies is exemplified by recent collections such as Cavalli-Sforza's (1986) edited volume and the symposium organized by Ellison and Bailey on the ecology and behavior of Efe and Lese populations from the Ituri Forest of Zaire, which appeared in the April 1989 issue of the *American Journal of Physical Anthropology*.

In spite of the fact that the African pygmies' most salient physical characteristic is their small size, their purported morphological distinctions (see Marquer, 1972, and Vallois and Marquer, 1976, and references therein) have never been the subject of detailed allometric investigation. In this paper, we analyze the allometric basis of African pygmy body proportions and consider the implications of our findings for the following three topics: morphology and climatic variation, retention of primitive morphological features, and the genetic and developmental basis of microevolutionary size change in human groups.

CLIMATIC ADAPTATION

Both the overall body size and specific body shape of African pygmies have been interpreted as evolutionary adaptations related to their inhabitation of hot, humid rain forests in Central Africa. Roberts' (1953, 1978) demonstration of negative correlation between body weight and mean annual temperature (Fig. 1), combined with Schreider's (1950) finding of a strong positive correlation between surface area-to-weight and temperature, has led many authorities to view the low weight of pygmies as an example of Bergmann's Rule. In this interpretation, the small overall size yields a high surface-to-volume ratio, thus increasing Newtonian cooling through heat loss (Hanna et al., 1989). Conversely, Roberts (1978), Cavalli-Sforza (1986), and others have argued that small size may be advantageous not because it enhances the dissipation of heat but rather because it yields reduced absolute rates of internal heat production. This perspective stresses that sufficient heat dissipation via sweating and surface cooling is problematic within the extreme humidity of the closed canopy of the Central African rain forest.

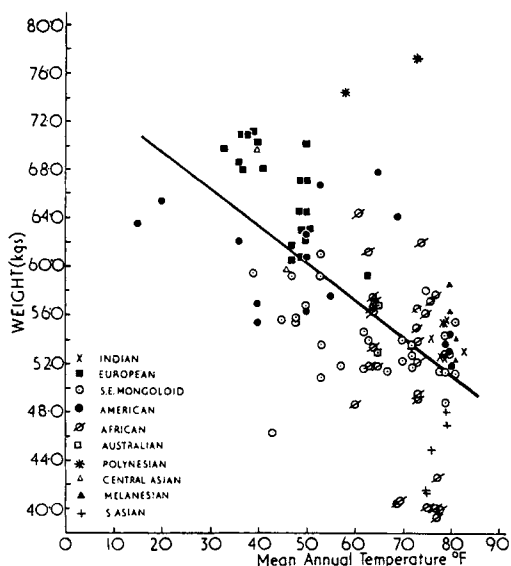


Fig. 1. A plot illustrating the negative correlation between body weight and mean annual temperature in human populations. African and Asian pygmy populations cluster below the trend in the lower right hand corner of the scatter. (Reproduced from Roberts, 1953, with permission of the publishers.)

Various specific body proportions of adult pygmies have also been interpreted as climatic adaptations. Hiernaux et al. (1975) showed that African pygmies have a low weight-to-height ratio (though, in fact, these variables exhibit a strong linear relationship across their 69 population means of West-Central Africans). They interpreted this aspect of body shape in African pygmies as a genetic adaptation selected to yield decreased ratios of weight-to-surface areas (see also Hiernaux, 1977). General discussions by both Roberts (1978) and Trinkaus (1981) suggest that the relatively long arms or distal segments of the extremities in pygmies and other tropical Africans are presumably related to increased efficiency in dissipating body heat, following Allen's Rule. Relatively shorter lower limbs in pygmies have also been offered as evidence of climatic adaptation in discussions of the "pygmoid" Twa (Tumba Lake, Zaire) for both women (Pagezy, 1978) and men (Ghesquiere and Karvonen, 1981), although the exact functional basis of this claim is not clear.

Finally, in extensive studies of the relationships between morphology and climate in sub-Saharan Africa, Hiernaux (e.g., 1968, 1974, 1977) and Hiernaux and Froment (1976) computed total and partial correlations between climatic variables and many specific anthropometric dimensions (e.g., shoulder and hip breadths, limb lengths, etc.) and indices (e.g., nasal, facial, cephalic). Roberts (1978) also computed many significant correlations between specific anthropometric variables and climatic data. The African pygmies represent very important data points in these comparisons, given their small size, particular morphology, and extreme habitat. Crognier (1981) has undertaken similar investigations on climate and anthropometric variation among populations from Europe, the Middle East, and North Africa.

ARCHAIC FEATURES AND PRIMITIVE RETENTIONS

A second body of work has differentiated African pygmies from other groups of Africans and non-Africans and suggested that they exhibit archaic or primitive morphological features. This position is best represented by the numerous studies of skeletal morphology and body proportions described and cited in Marquer (1972) and Vallois and Marquer (1976). For example, building on earlier work by Vallois (1927, 1940), Marquer (1972) concluded that the scapulae of African pygmies exhibit divergent and primitive proportions of breadth to height (actually length to width for Schultz, 1930; see Shea, 1986). She also noted that pygmy scapulae have axilloglenoid angles which indicate "a more marked cranial orientation than in all other human populations and, moreover, suggest an approximation to the Anthropoids" (Marquer, 1972, p. 91, our translation from the French). Marquer (1972, p. 112) also notes that an elongation of the distal relative to proximal segments of the extremities, and the upper relative to lower limb, are characteristic of the African pygmies. This set of morphological distinctions is viewed as "primitive or archaic in the sense that they are only found in exceptional cases in living human populations and be-

cause some also recall . . . the particular morphological disposition of the great apes, while certain others are uniformly found in the first hominids" (Marquer, 1972, p. 115, our translation). In sum, while such explanations do not necessarily rule out climatic adaptation, it is clear that these authors are primarily suggesting that African pygmies have retained primitive morphological features that have been lost in other human groups.

DEVELOPMENTAL BASIS OF SIZE REDUCTION

Recent research on the genetic and developmental basis of dwarfing in African pygmies and other mammals provides a third area of significant interest to physical anthropologists. Our understanding of this topic has been advanced considerably in the past several years, and new developments occur regularly. A brief introduction to the endocrine control of growth is a prerequisite to the following discussion (see Fig. 2, and Rimoin and Horton, 1978, Rechler et al., 1987, or Merimee, 1989, for details). Primary endocrine control of somatic growth is established by the secretion and circulation of growth hormone (GH), a large polypeptide molecule with multiple effects on cell division and metabolism. GH is synthesized and secreted by the somatotrophic cells of the anterior pituitary gland. This secretion is regulated by the interaction of two hypothalamic hormones, growth hormone-releasing factor (GHRF) and growth hormone inhibitory hormone (somatostatin), which in turn are regulated by a variety of humoral and central nervous system feedback controls. GH travels from the pituitary to all cells of the body, where it binds to specific growth hormone receptors (GHR), which are widely distributed. After GH binds to the receptor on the cell membrane, it circulates with a carrier protein known as high-affinity growth hormone-binding protein (GH-BP), which appears to be the extracellular portion of the GHR dissociated from the cell. Serum levels of high-affinity GH-BP can be assayed, and are thought to provide an indirect measure of the number of GHR present and active (Baumann et al., 1989).

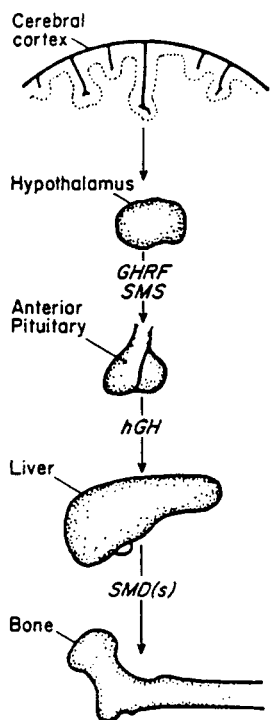


Fig. 2. The GH axis. GHRF = growth hormone releasing factor; SMS = somatostatin or growth hormone inhibitory factor; hGH = human growth hormone; SMD(s) = somatomedins, or insulin-like growth factor 1. See text for discussion. (Reproduced from Rimoin and Horton, 1978, with permission of the publisher.)

The effect of GH on growth appears to be primarily or totally indirect and is mediated through insulin-like growth factor 1 (IGF-1), which is a potent mitogenic growth factor essential for systemic and local growth (Froesch et al., 1985). GH binding induces the differentiation of stem cells to committed cells that are sensitive to IGF-1, and regulates local expression of IGF-1 genes, resulting in cell multiplication and growth. IGF-1 controls cell division (and ultimately, growth) by allowing cells to enter the "S" phase of the cell cycle, or a period of DNA synthesis (Leof et al., 1982). IGF-1 acts through some combination of autocrine, paracrine, and endocrine mechanisms. From the foregoing outline, it is clear that retarded growth and a similar small phenotype may be produced by a considerable variety of ge-

netic and epigenetic perturbations (see Shea, 1992).

Numerous explanations for the small size of African pygmies have been posited, ranging from simple nutritional effects to distal subresponsiveness to normal levels of GH (Merimee et al., 1968). At the present time, it seems clearly established that African pygmies have reduced levels of IGF-1 throughout growth (Merimee et al., 1987). This reduction in IGF-1 is associated with low levels of high-affinity GH-BP (Baumann et al., 1989), indicating a reduced number of GHR in the tissues of African pygmies. Recently, studies of Efe pygmy T-cell lines have shown resistance to the growth-promoting action of IGF-1, suggesting a lack of IGF-1 receptors (Geffner et al., 1993, 1994). Whatever the precise hormonal mechanisms ultimately determined to underlie the reduced body size in pygmies, their effects appear to be exhibited throughout the entire span of postnatal growth (Bailey, 1991a) and not simply during or just prior to puberty, as previously claimed by Merimee et al. (1987). This is just what would be expected of an alteration involving IGF-1 levels and/or distal subresponsiveness, since the predominant effects of this important mitogen are seen postnatally (e.g., Rechler et al., 1987). Figure 3 plots growth data for Efe pygmies of known age against comparative samples of Lese farmers and U.S. females, illustrating the reduced growth rate during even early postnatal growth.

In regard to genetics, Bowcock and Sartorelli (1990) have recently shown that there is no alteration or deletion in the regulatory sequence of the IGF-1 gene, and no differences in the distribution of IGF-1 alleles, in African pygmies vs. nonpygmy black Africans. The work by Merimee et al. (1990) suggesting that the short stature in African pygmies results from a failure of cellular GHR to increase in a normal manner may be most compatible with a change in a promoter gene regulating the expression of the GHR gene, rather than a structural defect in the coding region of the GHR gene itself (see Merimee et al., 1990, for additional discussion). It should be pointed out in regard to the recent finding by Geffner et al. (1993, 1994) that studies

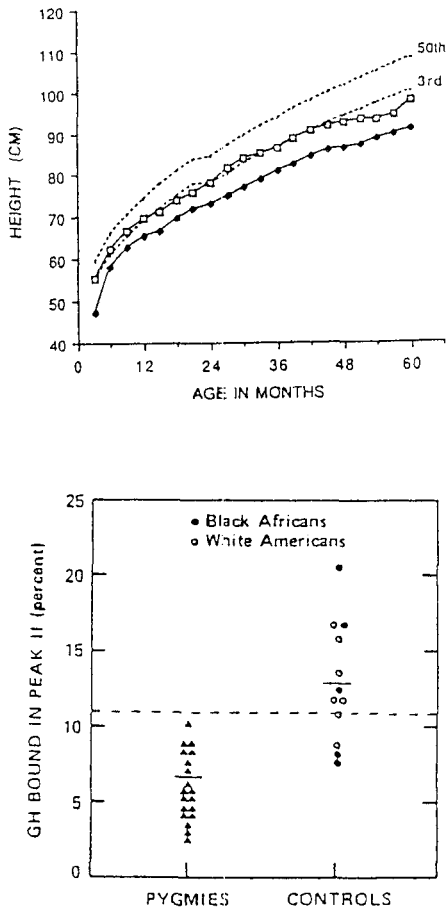


Fig. 3. **Top:** Mean height for age in Efe pygmies (black dots) compared to Lese farmers (white squares) and the 50th to 3rd percentiles for U.S. females. (Reproduced from Bailey, 1991a, with permission of the publisher.) **Bottom:** The percent of GH bound to the high-affinity binding protein in serum is indicated for samples of pygmies and controls. Pygmies have significantly lower GH-BP levels. (Reproduced from Baumann et al., 1989, with permission of the publisher.)

comparing the regulatory sequence of the IGF-1 receptor gene with that of nonpygmy populations have yet to be completed.

Our knowledge of at least some of the genetic and epigenetic bases of altered growth and reduced size in the African pygmies makes them a particularly attractive model for examining the effects of such developmental changes on body proportions. This provides a third significant rationale for our

study of growth and form in this group of modern humans.

COMPARATIVE ONTOGENETIC ALLOMETRY

As noted above, it is more than a little surprising in light of the prolonged anthropological scrutiny and the obvious small body size of the pygmies that no explicit allometric comparisons have been undertaken previously (this refers to studies specifically directed at pygmy body proportions, not those where attempts at size control in assessing other questions have included pygmy data points, such as the debates over australopithecine proportions and locomotor behavior: Jungers, 1982; Wolpoff, 1983a,b; Jungers and Stern, 1983). Nevertheless, the importance of this approach for understanding pygmy body proportions has been at least implicitly recognized by some, as for example when Huxley (1932) suggested in passing that the limb proportions of pygmies were likely an allometric correlate of their small size. More recently, Hiernaux (1974, p. 115) added the following qualification in delimiting relatively short legs, long arms, wide shoulders, and elongate distal extremities as characteristic of the Mbuti pygmies: "These, however, do not necessarily represent distinctive characteristics of the Mbuti independent of their short stature, since in any human population the shorter individuals tend to have relatively shorter legs, longer arms and wider shoulders."

Our primary goal in this paper is to further investigate Hiernaux's claim and to determine whether certain adult pygmy proportions in fact represent morphological novelties which are likely to be genetically and physiologically independent of the overall size reduction in these groups (whatever the functional implications of these proportion changes themselves). We illustrate the procedures we have utilized to address this question through a brief consideration of the concept of "allometric engineering" recently presented by Sinervo (1993). Imagine a hypothetical evolutionary scenario in which selection acts to decrease overall body size. Traits allometrically related to overall size

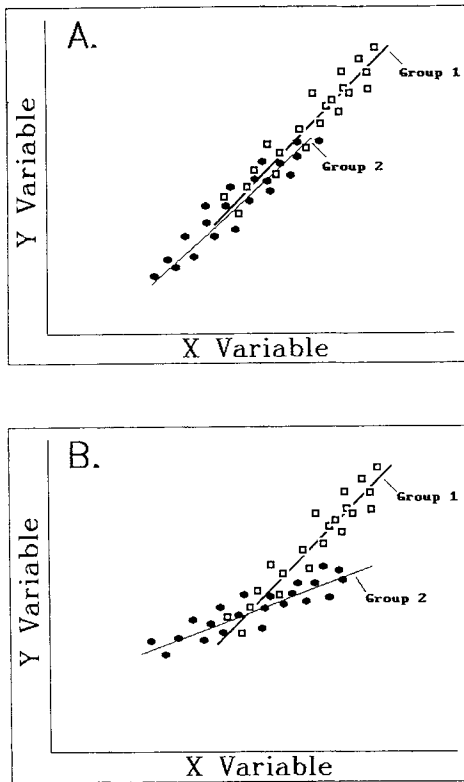


Fig. 4. A schematic representation of contrasting cases where proportions in a particular group (group 2, filled circles) result from simple allometric truncation relative to group 1 (A), vs. divergence of allometric trajectories in groups 1 and 2 (B).

via genetic, developmental, and physiological mechanisms will also change as correlated by-products of such selection.¹ Sinervo (1993, p. 211) calls these the "pure allometric effects of size." Figure 4A illustrates an example where the observed proportions in a new group coincide with these expectations. In contrast, Figure 4B illustrates a hypo-

thetical evolutionary scenario where the novel group does not coincide with these predictions. In such cases, we surmise that selection has independently operated on the Y variable to attain proportions in the observed range for comparable values of X. In other words, additional genetic changes (whatever their physiological bases or functional implications) have occurred in the Y variable, which are independent of the selection for overall size change and its genetic, developmental, and functional underpinnings. Here the intergroup adult correlation of Y with size may reflect either spurious correlation (Sinervo, 1993) or true biomechanical scaling (Gould, 1966), but not the pure effects of features developmentally linked to overall size via common growth controls.

How does one operationalize this allometric model? Sinervo's own "allometric engineering" approach experimentally manipulates egg size in lizard hatchlings as a way of determining the predicted trajectory of the allometric correlates of size change (Sinervo, 1993; Sinervo et al., 1992). Quantitative geneticists predict this trajectory based on empirically derived knowledge of genetic covariance of certain features with each other and overall size (e.g., Lande, 1979). Genetic engineering permits a determination of this trajectory when various genes controlling growth physiology are introduced, as in the case of allometric patterns observed in *MTrGH* giant mice exhibiting high GH and IGF-1 levels (Shea et al., 1987, 1990). Finally, comparative biologists can determine this trajectory by examining patterns of phenotypic covariance during ontogeny and utilizing ontogenetic scaling as a criterion of subtraction (Gould, 1975; Shea, 1981, 1985b).² The most robust statistical test of ontogenetic scaling is an analysis of covari-

¹We must stress the important distinctions between this type of allometric covariation, generated by ontogenetic scaling, and broad-based allometric patterns reflecting biomechanical scaling. The latter normally depart from ontogenetic scaling and indicate the need to adjust body proportions as size increases in order to maintain functional equivalence in some specific biomechanical parameter, such as peak strains reached during a particular type of locomotion. In biomechanical scaling, allometric covariance is not an automatic (pleiotropic) by-product of size change, but rather the specific result of selection for altered proportions in the new size range. See Gould (1966) and Shea (1981, 1984, 1985b) for further discussion.

²The major assumption involved in this procedure is that patterns of phenotypic correlation accurately mirror those of genetic correlation. It is the latter which will determine the actual evolutionary trajectories for features genetically linked to overall or regional size (Lande, 1979). In this regard, Cheverud's (1988) comparison of phenotypic with genetic correlation matrices demonstrated a strong correspondence; where the patterns differed, Cheverud concluded that the most likely basis for disparity lies in the inaccuracy of the genetic matrices due to inadequate sample sizes.

ance (or principal components analysis) based on ontogenetic data for all species; in other cases, we may have to simply ascertain whether adult values in the transformed group lie within the observed (truncated) or expected (extrapolated) range of the other species.

In the present study, we examine a "natural experiment" of "allometric engineering" where some of the physiological bases of the size change are largely known. Our null hypothesis is that any differences in adult proportions between female vs. male pygmies, or pygmies as a group vs. other groups, result from the simple extension of common patterns of ontogenetic allometry to larger terminal sizes. Our criterion for the rejection of this hypothesis is a marked departure from the expectations of ontogenetic scaling, a pattern concordant with the argument that selection has operated on individual dimensions or proportions independently of the changes in overall size.

MATERIALS AND METHODS

Samples

Efe pygmies—Ituri Project. Subjects measured for this study were drawn from a larger population of 470 nomadic Efe pygmies and 450 village-living Lese horticulturalists living in the Ituri Forest of northeast Zaire. Since 1980, these groups have been the subjects of the longitudinal, multidisciplinary Ituri Project. Additional information on the demography, nutrition, health, development, work activities, social relations, land use, reproductive ecology, and physical growth of these groups can be found elsewhere (Bailey and DeVore, 1989; Ellison et al., 1989; Bailey and Peacock, 1988; Bailey et al., 1989; Bailey, 1991b). The subjects included in the present study were residing in forest camps situated within 6 hours' walk of the Ituri Project research station during August 1987. The distribution of the total sample of 119 individuals by sex and age group is given in Table 1. Birth dates of those subjects under the age of 5 were known. The ages of older subjects were estimated using methods that are independent of physical maturation (see Bailey, 1991a, for details). Since this is an investigation of allometry or

TABLE 1. Sample size and mean heights and weights for the Efe sample arranged by sex and lumped age categories¹

Sex	Age	No.	Height	Weight
F	1	17	94.5	13.9
F	2	10	122.9	25.9
F	3	8	138.4	37.8
F	4	10	140.5	41.1
F	5	8	136.5	35.3
M	1	22	89.4	13.1
M	2	14	128.6	29.4
M	3	7	146.5	43.1
M	4	5	148.9	45.4
M	5	6	145.1	42.3
M	6	5	145.4	42.1

¹ Age categories given as 1 (10 years or less), 2 (11–20 years), 3 (21–30 years), 4 (31–40 years), 5 (41–50 years), and 6 (51–60 years). Two individuals in the female sample and five in the male sample have no known or estimated age given and are therefore deleted from this table. They are, however, included in the allometric analyses.

relative growth, our primary concern is the interrelationship between proportions and size, not age. We include these data here for general interest and to provide a summation of the sample.

Comparative sample. The monograph published in 1922 by Jan Czekanowski contains the results of one of the most extensive anthropometric surveys ever undertaken. Czekanowski and his colleagues measured thousands of individuals from numerous ethnic groups throughout Central Africa, in the area formerly known as "German East Africa", and including portions of what is now eastern Zaire, Rwanda, Uganda, and Tanzania. This German Central African Expedition published an extensive anthropometric database (66 variables and measurements) for 450 individuals, and an abbreviated compilation (19 variables and measurements) for 4,451 individuals. All individuals measured were adult males, and are identified by village, group, clan, and individual name. Czekanowski's (1922) monograph provides additional information, including maps, detailing the precise locations of the anthropometric surveys for those who are interested in these data.

Measurements

Efe pygmies—Ituri Project. In addition to age, weight, sex, and subject's name, a series of anthropometric measurements were taken by R.C. Bailey. These measurements were taken following the definitions and

methods described by Cameron (1986). The measurements include body height, height to the sternum, total arm length, upper arm length, forearm length, biacromial width, biliocrisal width, and height to the anterior superior iliac spine (ASIS). These measurements were chosen to address particular questions, such as relative limb lengths, and to correspond with certain standard dimensions prevalent in the literature.

Comparative data. Measurements used by Czekanowski's group were the same as those subsequently published by Martin (1914). The monograph provides no information regarding the actual measurers, or whether tests for intra- and interobserver error were undertaken. The set of measurements taken by us and also available in Czekanowski's monograph includes total height, height to the sternum, total arm length, upper arm length, forearm length, biacromial width, biliocrisal width, and height-to-ASIS. We cannot directly assess or control for potential differences in measurement technique between the two studies. Therefore, we utilized a simple indirect approach based on the fact that Czekanowski's data set includes mean values for various groups of adult pygmies. If the pygmy data points from Czekanowski's set of means fell comfortably within our cluster of adult Efe points, then we accepted the measurement technique as being adequately comparable to our own. This procedure does not bias our study toward acceptance of the hypothesis that adult nonpygmies lie along an extrapolation of the pygmy growth trend, since in cases where this prediction clearly does not hold, the nonpygmies will deviate significantly from this position regardless of where the Czekanowski pygmy data fall. On the basis of this approach, the only measurements which we ultimately rejected due to apparent incomparability of technique were forearm length (a slight difference) and biliocrisal diameter (a more marked difference).

In our statistical analyses and plots, we utilized the mean values included by Czekanowski (1922) along with the individual records for each "group," which was generally defined as being from a particular village or

site. Sample sizes on which these means are based are quite variable, ranging from several to 30 or more individuals.

Analyses

Differences in absolute size and proportions (ratios) between adult males and females were determined using t-tests in the Systat (Wilkerson, 1988a) statistical package. Differences in scaling patterns between male and female Efe growth series were tested using the analysis of covariance (ANCOVA) in the Systat (Wilkerson, 1990a) and Sygraph (Wilkerson, 1990b) statistical packages. We utilized significance levels of $P < .01$ for both our univariate and scaling contrasts due to the multiple-testing framework of our study. The ANCOVA procedure is based on least-squares regression analysis and allows one to test for differences in slope values and, if no differences in slope exist, intercept or position differences. The interesting and important continuing debates (e.g., Ricker, 1973; Rayner, 1975; Plotnick, 1989) over the most appropriate line-fitting techniques for studies of allometry and scaling apply primarily when the goal is to model a particular structural relation and perhaps test the observed value against some theoretically predicted slope. With samples of this size, and when the primary goal is to test for differences in patterns of growth allometry in two or more groups, ANCOVA is considered a very robust and preferable approach (Plotnick, 1989).

We supplemented the previous analyses with tests for significant differences in reduced-major-axis slopes (Clarke, 1980) in those cases where least-squares slopes differed. Position differences determined from ANCOVA analyses were retested using Tsutakawa and Hewett's (1977) "quick test." The statistical differences reported in Table 3 are those where both of these approaches revealed concordant results.

Adults represent a key portion of the total ontogenetic trajectory, and thus should be routinely included with young children, juveniles, and subadults in studies of growth allometry. However, if samples are disproportionately composed of adults, and adults in fact have a significantly different scaling pattern than other components of the entire

ontogenetic trajectory, this could yield confusing results. This point about differential sampling and scaling differences applies to any component(s) of the entire ontogenetic trajectory of course, and not just the adult sample (see Cock, 1966, for further discussion). To assess these potential effects in our sample, we divided the sequence into adult vs. subadult (young, juvenile, subadult) components and ran ANCOVAs for our various bivariate comparisons. None of the scaling patterns differed significantly between adults and nonadults, a result which confirmed our perception based on careful visual examination of the scatters. These analyses justify the use of the entire Efe sample to characterize patterns of growth allometry in this group.

To test the null hypothesis that adult nonpygmy values lie along an extension of the ontogenetic allometry observed in the Efe, we had to compare selected adult values from the literature with our empirically determined ontogenetic trajectories. We utilized two complementary approaches, one bivariate and one multivariate, to test this. First, we plotted 95% and 99% predicted intervals on the y values given observed x values for our Efe growth data scatters, extrapolated these prediction intervals into the size range of the adult literature values (these ranges overlap, actually, since the literature values include pygmy and nonpygmy means), and then determined whether the literature values fell within these prediction intervals. It is important to bear in mind the difference between a confidence interval (also termed the confidence interval for the regression, depicting the range where the regression line values will fall a specified percentage of the time for repeated measurements) and the prediction interval (also termed the confidence interval for the population, depicting the range where data values will fall a specified percentage of the time for repeated measurements). When assessing whether a particular specimen or group falls within the "expected" range (as specified by the significance level) for a given bivariate trajectory, it is the prediction interval which defines the relevant boundaries. Our Figures 5 through 9 include the confidence intervals for both the regression and

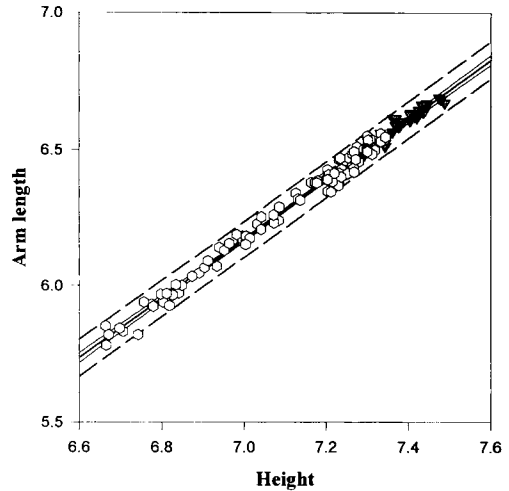


Fig. 5. An allometric plot of total arm length against height in the Efe ontogenetic sample (open hexagons) and literature means for pygmy and nonpygmy males from East Africa (stippled triangles). The least-squares regression (thick line) and 99% confidence intervals for the regression (solid lines) and population (dashed lines) are shown. Note the concordance of the adult literature values for nonpygmies with the prediction of ontogenetic scaling of the Efe trajectory.

the population; these were determined using Jandel's SigmaPlot graphing software.

We did not supplement these approaches with ANCOVA contrasts of the scaling patterns for our Efe ontogenetic series compared to a line fit to the pygmy plus nonpygmy adult means from Czekanowski (1922). This is because of the well-known theoretical and statistical difficulties involved in assuming that a static adult scatter (such as that derived from the Czekanowski data) will necessarily resemble trajectories of growth allometry (e.g., Cock, 1966; Shea, 1981, 1983a; Cheverud, 1982). However, since direct comparison of respective ontogenetic allometries is clearly the optimal approach, we qualify our results in this paper by acknowledging their preliminary nature and stressing the need for additional ontogenetic information for nonpygmy groups. Shea and Pagezy (1988; unpublished results) have produced such an analysis for a comparison of Twa pygmies and their Oto neighbors.

The final approach we utilized for assessing the concordance of adult literature

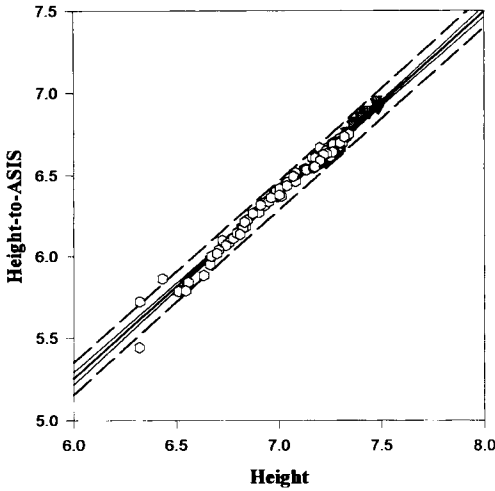


Fig. 6. An allometric plot of total arm length against lower limb length (height-to-ASIS ratio). Symbols, line fit, and confidence intervals as in Figure 5.

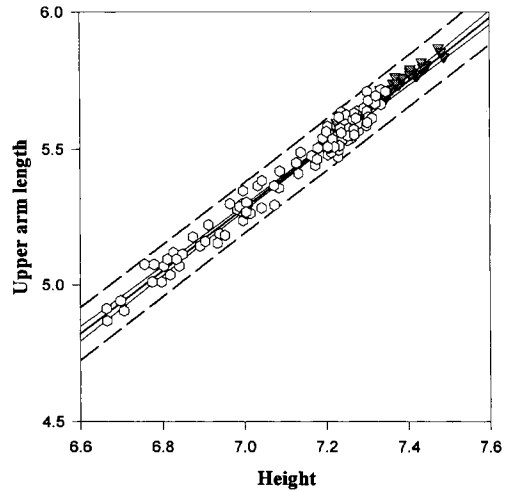


Fig. 8. An allometric plot of lower limb length (height-to-ASIS ratio) against height. Symbols, line fit, and confidence intervals as in Figure 5.

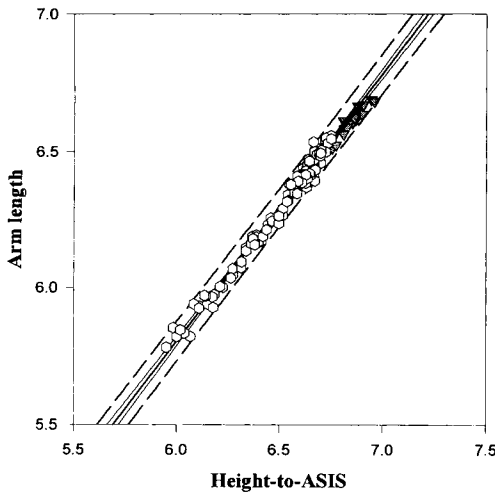


Fig. 7. An allometric plot of upper arm length against height. Symbols, line fit, and confidence intervals as in Figure 5.

values with the ontogenetic trajectories of the Efe was principal components analysis (PCA). PCA involves a rigid, geometric rotation of the original axes, resulting in a new set of axes where the maximum variation is expressed in a first composite principal component, with subsequent components being orthogonal and accounting for progressively less of the remaining variability (Al-

brecht, 1978). In the context of comparative studies of allometric growth among closely related groups, a pooled PCA will often result in a first component which effectively encompasses the allometric variation resulting from ontogenetic scaling among groups, while the second and subsequent components summarize group divergences in allometric patterns (see Shea, 1985a). A hypothesis of multivariate ontogenetic scaling for all dimensions would predict no significant separation of groups on the second or subsequent principal components in a multigroup analysis. Once again, however, it would be far preferable to have ontogenetic data for all groups in the PCA, and thus we emphasize the preliminary nature of these results as well.

RESULTS

Male vs. female Efe proportions and growth

Adult size and proportion differences. Table 2 presents adult (20 years or older) data for a series of anthropometrics (including weight) and proportion (ratio) variables determined from the same y and x variables used in the regression comparisons in Table 3. Body weight and all linear anthropometrics except biiliocrystal diameter are

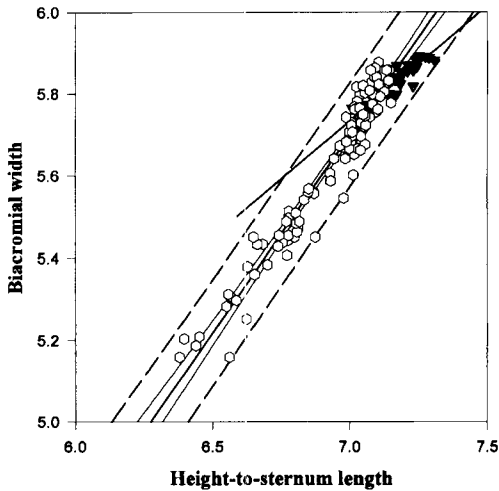


Fig. 9. An allometric plot of biacromial width against height to the suprasternal notch. Symbols, line fit, and confidence intervals as in Figure 5. An additional regression line has been fitted to the adult literature values to illustrate the near departure of the adult literature values from the predictions of the Efe ontogenetic trajectory.

significantly larger in adult males than females.

The selected contrasts reveal a number of differences between proportions of the adult males and females. For example, relative to weight, males have longer upper limbs (in both forearm and upper arm), broader biacromial diameters, and narrower biiliocrystal diameters. Proportion comparisons among the linear measurements indicate that males have longer arms relative to total height, height-to-sternum, and height-to-ASIS (or roughly lower limb length). Ratios of both forearm and upper arm lengths relative to these body heights are absolutely larger in males than females, although these differences reach statistical significance at $P < .05$ only for the upper arm/height-to-ASIS ratio. The ratio of biacromial diameter to biiliocrystal diameter is significantly larger in the males, exhibiting the largest t values. Of the remaining proportion contrasts summarized in Table 2, the next most significant intersex difference is found for the ratio of limb lengths (with lower limb length being estimated by height-to-ASIS). Males have relatively longer upper limbs, or females have relatively longer lower limbs,

depending on how one states the proportion difference.

Scaling patterns vs. body weights and selected dimensions. Table 3 summarizes the results of comparisons between male and female patterns of ontogenetic allometry among the Efe. Since there are almost no significant differences in slope or intercept values between males and females (see below), a pooled slope will provide an appropriate description for the scaling trajectories. Examination of the slope values for the linear dimensions against weight indicates a scaling pattern of slight to moderate positive allometry in both sexes, the only exception being biiliocrystal breadth in males. Correlation coefficients for the regressions on weight are quite high, generally being above .970, with the lowest being .941. The highest coefficients of growth allometry are observed for height-to-ASIS (basically a measure of lower limb length); moderate positive allometry is also exhibited for the arm vs. weight comparisons. Given this allometric pattern exhibited during growth and in an intersex comparison of Efe adults, a relatively longer-limbed body build would be generated by increasing overall body weight and size.

Proportion changes based on selected linear comparisons are also summarized in Table 3. These exhibit very high correlations, with little difference between least-squares and reduced major axis slope values. Arm length, upper arm length, forearm length, and lower limb length (height-to-ASIS) all increase with significant positive allometry relative to total height. This again accentuates the trend toward increasing relative limb length with increasing size. A regression of arm length against lower limb length (height-to-ASIS) yields isometric slopes. This finding is not expected considering that adult ratio values of arm/height-to-ASIS indicate a significantly higher value for males (Table 2); this may result from the higher (though not statistically different) male slope. This disparity is even greater in a comparison of male and female slopes for static adult regressions, though it still does not reach statistical significance, and plots of the adult scatters suggest marked concordance.

TABLE 2. Means, standard deviations, and *t*-tests for sex differences in adult *Efe* pygmies¹

Variable or ratio	Female (n = 26)		Male (n = 23)		t value	Probability
	M	S.D.	M	S.D.		
Age	34.70	8.30	39.7	10.50	-1.89	NS
Height	138.63	3.99	146.40	5.55	-5.67	**
Height-to-sternum	112.92	3.64	119.70	5.07	-5.42	**
Arm	61.12	2.41	65.77	3.21	-5.71	**
Upper arm	25.67	1.09	27.64	1.82	-4.66	**
Forearm	21.03	1.00	23.00	2.72	-3.43	**
Biacromial diameter	30.65	1.84	33.29	1.74	-5.15	**
Biiliocrystal diameter	22.82	1.07	22.93	1.02	-0.34	NS
Weight	38.27	4.43	43.20	4.73	-3.76	**
Height-to-ASIS	75.88	2.82	79.96	3.70	-4.37	**
Weight ³³	3.37	0.13	3.50	0.14	-3.57	**
Height/weight ³³	41.24	1.34	41.81	1.02	-1.67	NS
Sternum/weight ³³	33.58	1.11	34.18	0.99	-1.96	NS
Arm/weight ³³	18.18	0.81	18.81	0.68	-2.85	*
Upper arm/weight ³³	7.61	0.37	7.89	0.37	-2.40	NS
Forearm/weight ³³	6.25	0.30	6.56	0.72	-2.01	NS
Biacromial/weight ³³	9.11	0.41	9.50	0.33	-3.67	**
Biiliocrystal/weight ³³	6.81	0.28	6.55	0.30	-2.97	*
ASIS/weight ³³	22.57	0.92	22.83	0.69	-1.10	NS
Arm/sternum	0.54	0.02	0.55	0.01	-2.26	NS
Arm/height	0.44	0.01	0.45	0.01	-2.69	*
Forearm/height	0.15	0.01	0.16	0.02	-1.58	NS
Arm/ASIS	0.81	0.02	0.82	0.02	-3.44	**
Forearm/ASIS	0.27	0.01	0.28	0.02	-1.72	NS
Upper arm/ASIS	0.34	0.01	0.35	0.01	-2.40	NS
ASIS/height	0.55	0.01	0.55	0.01	-0.42	NS
Biacromial/biiliocrystal	1.34	0.07	1.45	0.08	-4.66	**
Biacromial/sternum	0.27	0.01	0.28	0.01	-1.95	NS
Biacromial/height	0.22	0.01	0.23	0.01	-2.30	NS
Upper arm/height	0.19	0.01	0.19	0.01	-1.86	NS
Upper arm/forearm	1.22	0.05	1.21	0.09	-0.55	NS

¹ Intersex comparisons are made for the basic variable set, ratios vs. $\sqrt[3]{\text{weight}}$, and selected linear proportions.

*.01, **.001; NS, no significant difference.

As noted, the results of the ANCOVA revealed almost no significant differences between the sexes in either slope or position values at $P < .01$. The exceptions to this trend are the higher male slope value for the regression of biacromial diameter on biiliocrystal diameter, and the higher female intercept value for the regression of arm length on height-to-sternum. It is worth pointing out that male slopes were generally higher than those for females in regression comparisons of the linear dimensions vs. body weight, although none of these differences reached significance at the $P < .01$ level. This pattern of higher male slopes was not observed for the linear proportion comparisons. This may reflect differences in body composition and higher female weights at comparable linear dimensions. Additional support for this explanation is provided by the fact that P values for intersexual differences in the regressions comparing linear dimensions are much higher (i.e., farther

from statistically significant ranges) than those for scaling patterns relative to body weight, with the exception of the biacromial vs. biiliocrystal diameters comparison noted above.

The finding of marked concordance of male and female patterns of growth allometry indicates that observed differences in adult proportions between the sexes result from the differential extension of common growth trajectories. In those cases where adult males and females do not differ in proportions, this merely reflects the fact that coefficients of growth allometry are closer to isometric values and/or the degree of overall size differentiation is not great enough to yield significant differences in terminal proportions.

Efe ontogenetic trajectories and adult literature values

Figures 5 through 9 illustrate the prediction intervals fitted to the Efe allometric tra-

TABLE 3. Results of regression analyses and ANCOVA for slope and position (intercept) differences between growth patterns in male and female Efe

Comparison		Slope (s.e.) ¹	RMA ²	Intercept (s.e.)	r ³	ANCOVA*	
						Slope	Intercept
Height*weight	F	.389 (.013)	.401	3.525 (.044)	.971	NS	NS
	M	.421 (.009)	.427	3.420 (.029)	.986		
Sternum*weight	F	.388 (.014)	.400	3.324 (.046)	.970	NS	NS
	M	.414 (.014)	.425	3.239 (.047)	.974		
Arm*weight	F	.386 (.015)	.400	2.716 (.051)	.964	NS	NS
	M	.434 (.012)	.444	2.571 (.041)	.978		
Upper arm*weight	F	.409 (.017)	.426	1.764 (.056)	.960	NS	NS
	M	.457 (.015)	.470	1.613 (.050)	.973		
Forearm*weight	F	.415 (.017)	.432	1.542 (.057)	.960	NS	NS
	M	.439 (.022)	.466	1.486 (.073)	.941		
Biacromial*weight	F	.379 (.015)	.393	2.046 (.049)	.964	NS	NS
	M	.423 (.011)	.431	1.917 (.037)	.982		
Biiliocrystal*weight	F	.385 (.014)	.396	1.721 (.045)	.973	NS	NS
	M	.350 (.013)	.361	1.818 (.044)	.970		
ASIS*weight	F	.419 (.017)	.437	2.814 (.056)	.959	NS	NS
	M	.479 (.016)	.496	2.613 (.053)	.966		
Forearm*upper arm	F	.997 (.027)	1.015	-.191 (.085)	.982	NS	NS
	M	.952 (.040)	.995	-.035 (.124)	.957		
Arm*sternum	F	.980 (.020)	.990	-.517 (.093)	.990	NS	*
	M	1.000 (.015)	1.005	-.599 (.068)	.995		
Arm*height	F	1.073 (.022)	1.084	-1.174 (.104)	.990	NS	NS
	M	1.104 (.015)	1.110	-1.313 (.071)	.995		
Arm*ASIS	F	.976 (.018)	.984	-.112 (.075)	.992	NS	NS
	M	.987 (.017)	.995	-.146 (.070)	.992		
ASIS*height	F	1.117 (.019)	1.125	-1.178 (.091)	.993	NS	NS
	M	1.163 (.017)	1.170	-1.396 (.082)	.994		
Biacromial*biiliac	F	.949 (.048)	1.000	.457 (.141)	.949	*	NS
	M	1.129 (.045)	1.171	-.041 (.137)	.964		
Biacromial*sternum	F	.953 (.037)	.988	-1.090 (.170)	.965	NS	NS
	M	.960 (.034)	.990	-1.106 (.160)	.970		
Biacromial*height	F	1.036 (.036)	1.068	-1.692 (.175)	.970	NS	NS
	M	1.064 (.032)	1.089	-1.808 (.154)	.977		
Forearm*height	F	1.155 (.030)	1.174	-2.649 (.144)	.984	NS	NS
	M	1.138 (.043)	1.180	-2.544 (.208)	.964		
Forearm*ASIS	F	1.052 (.027)	1.069	-1.508 (.113)	.984	NS	NS
	M	1.022 (.041)	1.065	-1.359 (.172)	.960		
Upper arm*height	F	1.140 (.027)	1.156	-2.376 (.131)	.986	NS	NS
	M	1.171 (.026)	1.186	-2.518 (.128)	.987		

¹ Isometric values include 0.33 for comparisons vs. weight, 1.00 for linear comparisons.² Reduced major axis slope.³ Pearson's correlation coefficient.* $P < .01$, NS = no significant difference.

jectories, with adult pygmy and nonpygmy mean values from Czekanowski's data set overlaid on these. These figures illustrate the 99% confidence intervals for both the regression and population, but we stress that we get identical results (specifically, in terms of acceptance or rejection of the hypothesis of concordance with the predictions of ontogenetic scaling) at the 95% level. In all these comparisons, observed proportions in the adult nonpygmies clearly fall within the confidence interval of the population determined for the Efe growth trajectory. This pattern holds for comparisons of arm length vs. height (Fig. 5), arm length vs. height-to-ASIS (lower limb length; Fig. 6), upper arm length vs. height (Fig. 7), height-to-ASIS vs.

height (Fig. 8), and height-to-sternum vs. total body height. Arm length, upper arm length, and height-to-ASIS also fit this pattern when regressed against height-to-sternum. In all the preceding comparisons, our criterion of acceptance accords well with a careful visual inspection, i.e., the growth trends exhibit strong correlations, the literature pygmy means are located within our adult Efe cluster, and the literature non-adult means fall comfortably within the prediction interval along what appears to be a direct extension of the ontogenetic trend. The only comparison which seems to depart somewhat from this pattern of concordance is that of biacromial width vs. total body height (Fig. 9). Here Czekanowski's adult

values for both pygmies and nonpygmies fall within the prediction interval, but the non-pygmy means are shifted somewhat to the right of the Efe trajectory and look as if they do not fit the overall ontogenetic trend very well. Since the Czekanowski pygmy means fall squarely within the Efe adult scatter, this would seem to eliminate differences in measurement technique as the basis for this apparent difference, but we cannot be certain of this. In Figure 9 we have fitted a second regression in order to emphasize the relative positioning of the literature non-adults. We need additional ontogenetic data to confirm any apparent difference in this bivariate trajectory for these groups. In the meantime, a conservative position is to accept ontogenetic scaling on the basis of the prediction interval test which we have utilized throughout this paper. Given what we know about sexual dimorphism in biacromial width, looking carefully at the pattern of within-adult scaling in the Efe, and keeping in mind that the literature values are means about which significant individual scatter would be expected, our preliminary interpretation of this situation is that the marked variance in biacromial width relative to body heights within adults reflects marked sexual dimorphism resulting from allometric dissociation rather than ontogenetic scaling between the two sexes. Therefore, controlling for sex in the comparisons might yield a clearer concordance with ontogenetic scaling.

The PCA was carried out on six measurements (height, height-to-sternum, arm length, upper arm length, biacromial breadth, and height-to-ASIS). The first principal component accounted for 98.7% of the total variance, while the second component explained less than 1%. First component loadings are all positive and distribute the individuals and means according to overall size. Figure 10 illustrates a plot of component scores for the Efe plus literature values, with axes scaled to comparable values. No significant separation of the pygmies and nonpygmies is summarized by the second or subsequent components (although the variable loading most strongly on this component, biacromial breadth, is the only one exhibiting divergence from ontogenetic scaling

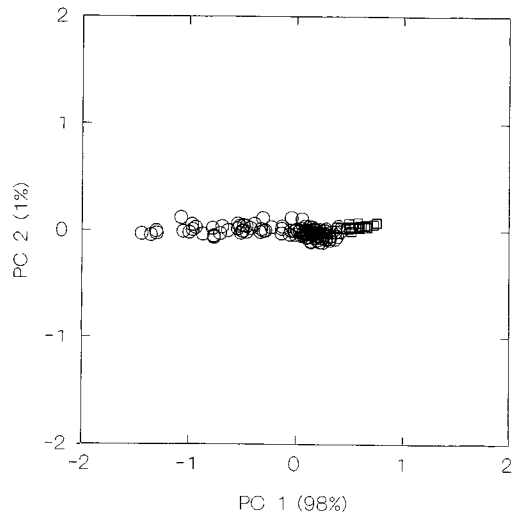


Fig. 10. Factor scores on the second vs. first principal components for the Efe ontogenetic series (open circles), Czekanowski adult pygmy means (asterisks, darkened area within the adult Efe range), and Czekanowski non-pygmy adult means (open squares). Note the relative placement along the first component of shared multivariate allometric change (98% of the total variance), and the lack of significant displacement between pygmies and nonpygmies on the second component of nonallometric divergence (1% of the variance).

in the bivariate comparisons). This general pattern of component eigenvalues, variable eigenvectors, and patterning of individual scores is consonant with generalized multivariate ontogenetic scaling (Shea, 1985a). However, we point out that these results should also be viewed as somewhat preliminary without full ontogenetic series for all the groups involved.

DISCUSSION

The results of this study suggest that the purported distinctiveness of body shape in African pygmies compared to other, taller populations arises primarily from allometric changes due to ontogenetic scaling. For the body dimensions examined here, and with the possible exception of relative biacromial width, adult pygmies are proportioned in comparison to adults of other groups just as we would expect, based on their smaller overall size and a general pattern of ontogenetic scaling. Such multiple proportion differences observed between the adult pygmy

vs. nonpygmy samples reduce to the correlated by-products of a coordinated allometric transformation.

In view of these findings, we now discuss, in inverse order, the three major topics introduced at the beginning of the paper.

Developmental basis of size reduction

Our finding of pervasive ontogenetic scaling of body proportions in the Efe fits both theoretical expectations (Katz, 1980; Shea, 1988, 1990, 1992) and previous empirical work in several areas. A variety of models of size change via shifts in levels of GH, IGF-I, and/or high affinity GH-BP yield results which corroborate our findings here. Shea (1992) has reviewed the endocrine control of size and allometric patterns elsewhere, but a few examples are worth stressing at this point. Size and shape changes in the organs (Shea et al., 1987) and skeleton (Shea et al., 1990; Oberbauer et al., 1992; Vogl et al., 1993; Wolf et al., 1991) of giant transgenic mice, characterized by overproduction of GH and IGF-I, result almost exclusively from allometric extrapolations. Siddiqui et al. (1990) demonstrated that in mice from lines divergently selected on the basis of plasma IGF-I levels, allometric factors account for the adult differences in relative weights of the carcass and skin plus viscera, as well as the proportions of protein, water, and fat. They conclude that "selection for high plasma concentrations of IGF-I therefore appears to produce a highly co-ordinated increase in body growth without influencing composition at equivalent weights. Whether this is a reflection of a co-ordinating role for circulating IGF-I in growth regulation awaits further study" (p. 157). Additional studies extending this work to relative organ size and skeletal dimensions provide further support for this general conclusion (Siddiqui et al., 1992). Other relevant examples and discussion are presented in Shea (1988, 1990, 1992).

This study of African pygmies, who are characterized by decreased levels of IGF-I and high-affinity GH-BP (plus possible IGF-I resistance), provides additional support for the hypothesis that pervasive pleiotropic effects on skeletal dimensions following a pattern of ontogenetic scaling are produced by

shifts in systemic GH levels controlling systemic and local production of IGF-I, GH-BP, and perhaps other growth factors. In other words, the multiple and allometrically coordinated changes in skeletal proportions in the pygmies mirror the pattern of simple genetic and growth perturbations observed in transgenic, mutant, and selected mice. Preliminary data on both hormone levels and the allometry of skeletal and anthropometric proportions in the short-statured Aeta of the Philippines suggest a very similar result (Shea et al., 1992). And although hormonal data are not available for these groups, analyses of anthropometric data in the pygmy Twa and neighboring Oto villagers of Lake Tumba, Zaire, also exhibit a predominant component of ontogenetic scaling (Shea and Pagezy, 1988).

These results fit with Katz's (1980) general model suggesting that shifts in systemic growth controls such as GH and IGF-I should yield simple allometric transformations. Presumably, it is more local growth control factors, such as those determining the number or size of germinal centers and intrinsically controlled local rates of cell division (Katz, 1980), that yield clear dissociations of allometric patterns (i.e., departures from ontogenetic scaling). For the morphologist dealing with terminal phenotypes, this means that complex and highly integrated patterns of proportion changes during growth and size shifts are determined by rather simple underlying controls. Consequently, a shift in terminal size will automatically yield a cascade of coordinated allometric alterations in local regions and anatomical proportions. These underlying genetic and developmental controls, and their gross phenotypic expression, must be fully understood when analyzing individuals, sexes, groups, or species which differ in body size.

In such a model, global allometric transformations will occur with body size changes through these genetic and developmental pathways, regardless of whether natural selection has driven the size change or not. Unless we have evidence to the contrary, we cannot rule out size change (along with allometric correlates) through genetic drift as the basis for some or all of the known cases

of human microevolutionary dwarfism. We should not merely choose among competing adaptive scenarios of size change without considering nonadaptive alternatives (Gould and Lewontin, 1979).

Heterochrony has played a key role in attempts to relate developmental processes and patterns of morphological transformation to micro- or macroevolutionary trends (e.g., DeBeer, 1940; Gould, 1977; McKinney, 1988; McKinney and McNamara, 1990). In this regard, it is interesting that one of the first invocations of neoteny, or evolutionary transformation via juvenilization, focused on human pygmies (Kollman, 1905). Our data on allometric patterns in the Efe (including the first reliable data on longitudinal growth-in-time—Bailey, 1991a), plus that emerging for other groups of small humans (e.g., Shea and Pagezy, 1988; Shea et al., 1992), yield a fairly clear picture of the heterochronic transformation involved here. The global ontogenetic scaling of allometries and reduced rates of body weight growth-in-time are indicative of the heterochronic transformation termed rate hypomorphosis (Shea, 1983b). Neoteny and time hypomorphosis (Shea, 1983b, or the progenesis of Gould, 1977, and other authors) will also yield a juvenilized or paedomorphic morphology. But in the first case, allometric patterns will not be coincident (or ontogenetically scaled) in the two groups, and in the second case, the duration of growth (and not merely the rate of growth-in-time) will be truncated, so that the transformed group will cease growth and become sexually mature at a significantly earlier age. Neither of these profiles fit the African pygmies (see Shea, 1989, for additional discussion of the role of rate hypomorphosis vs. neoteny in determining the morphology of pygmies). The significance here is not merely to describe and categorize, but rather to stress that the morphological distinctiveness of African pygmies appears to result from a type of allometric transformation which is likely the simplest in terms of required changes in genetic and developmental controls. Fundamental changes in allometric patterns or shifts in timing of growth cessation may require considerably more complex changes.

Archaic features and primitive retentions

Our allometric analyses allow a reconsideration of claims (e.g., Marquer, 1972) that proportion differences between pygmies and nonpygmies reflect the former's retention of features that have been described as primitive and more closely approximating the condition seen in early hominids or the great apes. The frequently discussed differences in proportions between upper and lower limb lengths, and between the elements within each limb, are in fact what would be predicted given generalized allometric truncation or ontogenetic scaling. As Hiernaux (1974) and Huxley (1932) surmised (see above), but did not examine, many of these disparate features need to be viewed as correlated consequences of the overall size change, and not independent developments. Our ontogenetic perspective allows a more detailed and explicit test of this possibility, confirming the allometric nature of purported pygmy distinctions. For those features in which the adult pygmies differ from other groups but in which they are ontogenetically scaled (as, for example, the relatively shorter lower limbs), we conclude that there is no more evidence for the retention of primitive, "archaic" or "apelike" features than in comparably sized small adults and subadults from other groups. We do not address in this paper all of the features discussed by Marquer (1972), Vallois and Marquer (1976), and others, particularly the skeletal proportions of the scapula and other areas of the postcranium. But we emphatically assert that, based on our results, a null hypothesis of allometric transformation via ontogenetic scaling should be assumed in all cases until fully tested and clearly demonstrated otherwise.

Our results also demonstrate how apparently quite divergent morphologies can in fact be easily generated through simple shifts in underlying genetic and developmental controls. This phenomenon is well appreciated in the broader literature on allometry and heterochrony in evolutionary biology (e.g., Gould, 1977; Raff and Kaufman, 1983; Thomson, 1988; McKinney, 1988). Quite simply, what may appear to the traditional anthropologist focusing on individual traits as per-

vasive and fundamental differences, are in fact the expected morphological result of size change and common truncation of myriad and integrated allometric trajectories.

This information can have substantial systematic implications when one is comparing related species (Shea, 1985b, 1992). In the present case of modern human populations, the implication is that pygmies are morphologically not very different from other groups once allometric factors are appreciated and analyzed. Needless to say, this morphological perspective fits well with a broad array of genetic data (e.g., Boyd, 1963; Cavalli-Sforza, 1986; Omoto, 1984, 1989) which rejects previous claims that the various short-statured groups from around the world represent closely related remnants of a once continuous and "primitive" stratum of humanity quite distinct from their more immediate and neighboring groups (e.g., Kollman, 1905; Romer, 1959; Howells, 1944; see Gusinde, 1955, and Gates, 1958, 1961 for additional discussion). It also accords with the recent contention that the current ecological and economic situation of pygmies may not be a product of millennia of cultural and biological adaptation to the challenges of the tropical rain forest environment, but rather a result of a more recent invasion of this environment by peoples economically linked with shifting cultivators and the new habitats created by them (Bailey et al., 1989). We can now be confident that body size decrease and its allometric consequences are a derived complex evolved multiple times in parallel among various human populations.

Climatic adaptation, size, and proportions

Comparative and correlational studies. The argument that the small overall body size and/or specific body proportions of human pygmies are the result of strong and sustained selection for thermoregulatory efficiency in hot and humid tropical rain forest environments is both long-standing and physiologically reasonable. However, this proposition clearly needs to be treated as a preliminary hypothesis. Most recent authorities have favored some version of the heat-adaptation hypothesis, but have also stressed that additional or alternative selective explanations might account for the mi-

croevolution of small body size in pygmies (e.g., Cavalli-Sforza, 1986; Omoto, 1984; Diamond, 1992). In assessing this question, we (like our predecessors) are primarily restricted to comparative approaches, since we cannot examine selection pressures directly, or experimentally analyze the impact of particular morphologies on fitness in natural habitats. In a few cases, however, the literature on climatic adaptation in pygmies does allow us to move at least somewhat away from standard comparative approaches and attempt to assess whether variation in experimentally tested performance criteria actually correlates with variation in morphology, an approach articulated by Arnold (1983) in his seminal paper on the study of adaptation. In the following discussion, the reader should bear in mind that hypotheses of climatic adaptation have often been forwarded for body proportions and body size independently, and an acceptance or rejection of climatic adaptation for one of these aspects of morphology doesn't require a similar decision for the other. Specifically, it is possible that a decrease in overall body size results from selection for thermoregulatory efficiency, but that proportion changes represent secondary and nonadaptive allometric correlates of this size change. We will discuss the issues related to proportion and overall size changes separately as follows.

Body proportions

Roberts (1953), Hiernaux (1977), and others have demonstrated significant correlations between climatic variables and individual dimensions or body proportions in pygmies and other African and non-African groups. Pygmies tend to be quite important data points on these correlational trends, due to their small size and the extremes of temperature and/or humidity in their rain forest environments. In our view, a claim of microevolutionary adaptation to a novel environment requires that the change in a given feature has been produced by the direct action of natural selection (Gould and Vrba, 1982; Baum and Larson, 1991), and is not the simple correlated consequence of selection acting on covarying features, such as body size in an allometric context (Huxley, 1932; Gould and Lewontin, 1979; Gould and Vrba, 1982;

Strauss, 1984; Shea, 1985b; Sinervo, 1993), or any other feature in a more general context. We do not favor a much broader and looser definition of adaptation, such as one basically equating it with function, or one that counts as an adaptation any feature that enhances fitness, regardless of its origin. Let us emphasize our keen awareness that in comparative studies we cannot ever be fully certain where selection has been, or is currently, active; all we can really determine in such studies is whether an observed pattern is consistent with a particular hypothesized selective scenario (or set of these). But we add one absolutely vital condition to such scenario building, i.e., that our explanation be guided by parsimony. Even if we cannot directly observe or precisely reconstruct the actions of selection and the development of true adaptations in comparative studies, we can guard against the invocation of more complex selective scenarios than are absolutely necessary in order to account for a particular observed pattern. The "simplest" scenario may not always be correct, but without additional information to the contrary, it is a basic and well-accepted scientific principle that the most parsimonious explanation is to be preferred (Sober, 1988), since it requires the fewest untested assumptions. In the realm of allometric change via ontogenetic scaling in African pygmies, this means that we do not accept as independent evidence for climatic adaptation any morphological feature or proportion correlated with climate but which is also interpretable as an allometric consequence of small size (cf. Strauss, 1984; Sinervo, 1993; see Introduction).³

A discussion of three relevant criticisms frequently leveled at such explanations based on "genetic/developmental allometric covariation" may provide further necessary

clarification here. First, it is often noted that allometric patterns of covariation themselves (and not merely size in isolation) are currently possible targets of selection; therefore, it is reasonable to assume that many or most ontogenetic allometries were in fact originally "built" through the direct action of natural selection on both variables in the past. These particular allometric trajectories, relative to other possible or observed ones, should be viewed as adaptations by our definition. We accept this argument regarding the adaptive origin of developmental allometric covariation as very likely true in most cases (Shea, 1985b), with the important caveat that this applies to the historically specific time of the origination of such patterns of allometric covariation. However, if and when such a system of covariation becomes held together through common genetic and developmental underpinnings, rather than persistent selection on the independent features, its continuation becomes a historical legacy of these common controls, and no longer the product of continued selection on both components in the system.⁴ As Gould (1992, p. 433; 1989, p. 537) recently stressed, Darwin fully recognized the significance for evolutionary change and notions of character adaptation raised by these "correlations of growth", even if he had to admit frustration at the relative lack of knowledge at that time as to the developmental and genetic factors underlying such linkages.

Just how do we ascertain whether such common genetic and developmental controls, rather than continued direct selection on both features, are responsible for persistent allometric covariation in a particular case? To understand how such allometric underpinnings might be recognized, the reader

³The distinctions between ontogenetic and biomechanical scaling are once again key here. Only cases of ontogenetic scaling yield correlated allometric changes which we would view as non-adaptive, or at least not independent evidence for adaptive change. In biomechanical scaling, selection has presumably directly acted on the Y variable to readjust proportions to the new biomechanical environment produced by the selection on the X, or size, variable. This is clearly adaptation by any definition, though the adaptive transformation in the size of y is perhaps best viewed as relative to the novel body size of the organism rather than the specific external environment.

⁴Frazzetta (1975) and especially Riedl (1978) provide an interesting discussion on the construction of adaptive and integrated suites of features, and how these systems become tied together in terms of developmental and genetic controls. Riedl (1978) notes how features that are initially variable and developmentally peripheral (and thus easy targets for independent response to selection) may subsequently become embedded in developmental matrices of many linked features (thus generating pleiotropy and yielding correlated effects). Such processes free natural selection from the constant burden of monitoring countless independent features. The historically directive or constraining influences of such covarying systems in producing correlated change not specifically generated by natural selection are great.

should refer to the discussion of Figure 4. Recall that the lab geneticist will artificially select only on size and then determine the correlated change in other features (where selection is clearly not operating in this controlled case); the quantitative geneticist calculates patterns of genetic covariation based on breeding histories and can then accurately predict (rather than directly observe) a response in a given feature that would be completely a correlated consequence of selection focused solely on another (e.g., Lande, 1979); the experimentalist will manipulate overall size in some direct fashion and determine the correlated consequences for other features not manipulated (Sinervo, 1993); and those studying naturally occurring or genetically engineered changes in single genes controlling general growth and terminal size can examine the covarying changes resulting in other specific features (e.g., Shea et al., 1987, 1990). All of these approaches will clearly fail to produce or indicate any correlated change in the Y variable when X is altered, if in reality the basis of the covariation between the variables is simultaneous selection on both variables independently.

The comparative morphologist's window into these issues is admittedly more restricted and less direct, but here knowledge of ontogeny becomes the key factor. The allometric changes in features which covary as size increases during growth in one species clearly are not the product of natural selection currently acting on the variance at one stage to yield that of the next stage. Rather, such an ontogenetic allometric trajectory reflects (save environmental influences) the genetically controlled program of growth characteristic of this individual species and inherited from its parent species. In cases of ontogenetic scaling, where between-group size and shape changes merely truncate or extend these ontogenetic changes within groups, we simply infer that the most parsimonious explanation of this pattern is that the same genetically controlled system of growth underlies the differences between the two groups. A pattern of ontogenetic scaling is consistent with a hypothesis of selection on size alone, or even size change via genetic drift (see Lande, 1979), as long as the

observed pattern of phenotypic covariance reflects the genetic correlation between the variables. In contrast, Zeng (1988) demonstrates that the predicted evolutionary or interspecific allometry will deviate significantly from ontogenetic scaling when selection on X is accompanied by any sort of selection (stabilizing or directional) on the Y variable. In this light, we see no reason to maintain a more complex scenario requiring assumptions of simultaneous selection on multiple features when quantitative genetic theory predicts an alternative trajectory and when a more simple explanation can account for the observed pattern, even if we, like Darwin, are relatively uniformed regarding the specifics of the genetic and developmental linkages.⁵ On the other hand, a departure from ontogenetic scaling is a pattern consistent with active selection (perhaps on both variables) to alter an ancestral system of growth controls in order to yield a new trajectory and/or terminal result. Because this pattern is more complex than in cases of ontogenetic scaling, a more complex explanatory framework than merely developmental allometric covariation is invoked to account for it.

A second criticism often raised against allometric hypotheses like the present one is that all changes must have some basis in ontogenetic modifications, and to merely determine these and suggest that something is "size related" does not obviate our need to investigate the consequences of such changes for function and/or fitness. Again, we generally agree with certain aspects of this position, but insist on making some further key distinctions. These distinctions are more vital to studies of evolutionary adaptation than to narrow functionalist biology; after all, functional biology does not require a Darwinian world view of transmutation via inheritance to address many of its basic

⁵Of course, if we understand something of the specific genetic and/or developmental controls underlying pleiotropic covariance (of allometric or other varieties), then we are in an even stronger position to conclude that a particular change in relative size of a Y variable is a correlated response. The role of systemic growth factors such as GH and IGF-1 in regulating both overall size and affecting many specific features in concert is key here for an understanding and proper interpretation of developmental allometry.

questions about "how structures work." First, virtually all the features of organisms that we examine, whether imbedded in a network of allometric covariation or not, "function" in various ways. However, we agree with the majority of recent theorists who stress that function does not equal adaptation, the latter requiring and reflecting the direct action of natural selection in a structure's origin or relative size change (Gould and Vrba, 1982; Gould and Lewontin, 1979; Baum and Larson, 1991; Lande and Arnold, 1983). These are not mere semantics of little relevance for comparative biology; in new environments it is the novel derived features driven by directional selection which are going to be of the greatest help in understanding the bases of evolutionary transformations (correlated changes and those produced via drift will only confuse our interpretations via their spurious correlation with the change in environmental factors). The demonstration that ontogenetically scaled transformations are non-adaptive correlates of other changes does not necessitate that such morphological shifts are without functional consequences (and certainly does not require that they are unadaptive), though any purported functional ramifications need to be explicitly demonstrated rather than merely assumed as is often the case in comparative studies (see below). Thus, an ontogenetic allometric perspective does not remove function, it highlights covariation, and therefore casts assumptions of the independence of features and hypotheses of adaptation in a different and more complete light. Many evolutionary biologists have recognized the importance of gaining such information in various realms of covariation (allometric and otherwise), and some specific analytical perspectives have been developed to attempt to separate direct and correlated responses to selection (e.g., Lande and Arnold, 1983). Huxley's (1932) developmental allometry is most appropriately viewed as one component of this general approach and perspective. Though recent polemical discussions (e.g., Gould and Lewontin, 1979) may have conditioned some evolutionary biologists to view such interpretations as heretical in their departure from traditional views, an essentially similar interpretation of developmental allome-

try and adaptation was offered by G.G. Simpson in his specific and more general discussions of this topic (e.g., Simpson, 1953, pp. 63–65, 286–287). As noted previously, Darwin himself explicitly discussed such growth correlations in juxtaposition to straightforward adaptive explanations for individual features.

A third criticism of allometric explanations often raised is why, given only an observed phenotypic covariance between size and another feature, one should argue for a correlated change in the Y variable linked to selection on X, to the exclusion of the converse, i.e., selection on Y with correlated change in X. Again, there is some legitimacy to this criticism, particularly in the absence of other information. The answer lies in the fact that overall body size is a feature developmentally regulated (in large part) by general and systemic growth controls, such as the GH and IGF-1 influences discussed above. The statistical correlation and covariance evidenced in an ontogenetic allometric plot of a given Y variable against some X variable (reflecting global or regional overall size) demonstrates only the covarying growth in Y which is regulated in common with X by these systemic growth controls.⁶ Myriad lines of evidence clearly indicate that in most or all cases there exist localized growth controls also affecting such Y variables, independent of the common controls affecting overall size. The relative influence of such factors (along with environmental influences) is revealed in the dispersion or scatter of individual values about the general trend. Considerable genetic, experimental, and comparative data reveal that selection can therefore quite effectively target changes in such features independent of correlated effects on X or overall size (as, e.g., demonstrated by Hooper, 1977, in selection experiments on long bone lengths and limb proportions). This is simply the most reason-

⁶This discussion assumes the common situation of plotting a local variable on the Y axis and a global one, such as overall weight, on the X axis. However, plots of local variables against one another, such as humerus length (Y) vs. femur length (X) are perhaps even more prevalent in allometric growth studies. Here the general correlation and pattern of covariance reflect a common response in both X and Y variables to a particular growth control.

able conclusion given our current best understanding of how global and localized controls of growth and morphogenesis are normally structured (e.g., Bryant and Simpson, 1984; Katz, 1980; Shea, 1990, 1992; Atchley and Hall, 1991). It is also fortunate for organisms undergoing selection for rapid changes in morphology, since such shifts would otherwise be impossible to generate without massive correlated responses in overall body size, with the well-known pervasive implications of such size shifts for almost all biological systems.

Returning to the issue of pygmy body shape and climatic adaptation, in addition to the proportions we have examined here, "leanness" and relative muscle mass have often been suggested as changes indicative of special adaptation to climate. For example, Cavalli-Sforza (1986, p. 398) notes his "superficial impression" and the common observation that pygmies "have especially thin calves, legs, and arms." But Hiernaux's (1977) plot of weight vs. height for adult Africans shows pygmies to lie right on the general allometric trend of strong correlation, and not significantly below it. Moreover, Dietz et al. (1989) found no difference in weight-for-height between Efe and Lese children. Bailey et al. (1992) present additional data to indicate that pygmies appear no leaner for their heights than other groups of Africans. Whether muscle mass itself is relatively reduced in pygmies is an issue that requires further investigation, but a marked deviation toward relatively lower weight/height ratios than expected in humans of their overall height would provide much more convincing support for the argument of increased capacity for heat loss (or decreased heat production) as a novel and independent development. For example, the clear specialization of highly linearized body form in modern Nilotics provides strong evidence of such a change, and thus more convincing support for the applicability of thermoregulatory explanations of body shape to this particular group (e.g., Ruff, 1991, 1993).

The preceding discussion can be abstracted as follows. We conclude that the most parsimonious explanation of the changes in body dimensions and specific proportions in the African pygmies examined

in this paper is that they are nonadaptive allometric correlates of overall size reduction, and they are not indicative of independent adaptive novelties individually selected in response to the demands of their rain forest environment. In this respect, we find ourselves in agreement with the dean of the thermoregulatory adaptationists, Jean Hiernaux, when he surmised that such body shape changes were in fact not independent of the more general reduction in pygmy stature and weight (see quotation in our Introduction). It remains to be determined exactly what, if any, functional changes co-occur with these allometric proportion shifts. We emphasize that whatever the inferred functional implications of an adult pygmy to nonpygmy contrast, they should be experimentally verified and also invoked in a comparison of subadult and adult nonpygmies.

Body size

Pygmy body size itself, rather than particular body proportions, has been the more common object of selective scenarios based on thermoregulatory adaptation and correlations with climatic variables. Our discussion at this point moves entirely into the realm of a critical analysis of previous arguments in this area. We stress that nothing in the allometric analyses presented in this paper directly informs us in any independent fashion about the ensuing discussion of hypotheses of thermoregulatory adaptation and overall body size. Similarly, an alternative interpretation of our assessments to follow in no way implies a rejection of our preceding arguments regarding the allometric covariance of body shape with overall size change. This is true regardless of the factors ultimately determined to be the cause of the overall size reduction in human pygmies.

Claims of evolutionary thermoregulatory adaptations⁷ in pygmies were originally

⁷We stress the term "evolutionary adaptation" here because we think it is important to distinguish between functional implications, which have actually been generated by selection in response to specific environmental challenges, and those which result from untargeted morphological changes. For example, size reduction in any human group, whatever the selective basis of its production, will yield higher surface area-to-volume ratios (true also for hypopituitary dwarfs and human subadults).

based on Bergmann's Rule and the law of surface areas to volumes. In this scenario, small body size was specifically selected for in the pygmies in order to increase the amount of surface area available for heat loss via convectional cooling. The unlikelihood of losing sufficient heat by this mechanism in the hot, humid rainforest has resulted in a shift toward the view that small size was selectively advantageous due to the absolutely (though not relatively) lower levels of heat production (e.g., Cavalli-Sforza, 1986; see also Lewin, 1991).

There is no question that there is a great deal of both theoretical and empirical support for the general association of body size and climate among modern humans. Ruff (1993, 1994) provides recent reviews of these arguments. However, we wish to raise some alternative points, particularly as these relate to human pygmies. First of all, while the overall inverse correlation between body size and climate is moderately strong in worldwide samples, often overlooked is the fact that Hiernaux's (1968) data do not support such a relationship between environmental temperature and weight in sub-Saharan African populations (though stature and sitting height do exhibit significant correlations). The lack of association between weight and climate here may simply reflect the fact that relative humidity, a key variable in climatic hypotheses, is not included.

Considering the pygmies more specifically, it could be argued that they fit the general pattern least well in Roberts' (1953) much-discussed plot of temperature vs. weight in modern humans (see Fig. 1). The pygmy groups have the greatest deviation from the line of best fit. In such correlational studies, a causal basis for the observed pattern of association is generally inferred by invoking a theoretical linking argument, in this case involving thermoregulation. It follows that the more closely a group's morphology accords with the correlational trend, the more relevant is that biomechanical linking argument in accounting for the group's relative placement in morphospace. Strong deviation from the predicted value presumably indicates measurement error, random variation, or the presence of other causes contributing to the placement of the group (indeed, this

is how deviations from allometric "best fits" are often explained in terms of nonallometric special adaptations). Pygmies may be small, but it appears that they are "too small" and deviate too much from expected values to provide, of themselves, much empirical support for the general causal explanation relating climate and body size.⁸ An alternative way of highlighting this point is simply to note the huge variance in body size (y-axis values) for a given x value of approximately 75–80°F. mean annual temperature in Figure 1. It is very important to stress here that one may question or reject the thermoregulatory adaptationist scenario as it applies to size change in the pygmies specifically, while still accepting the general applicability of this explanatory framework as applied to the pattern depicted in Figure 1. Moreover, the absence of relative humidity input into the climatic variable in Figure 1 may also account for some of the observed pattern of residualization from the general trend, particularly for those groups like the pygmies inhabiting humid rain forest environments.

An additional point to be considered in a comparative framework is the fact that not all groups of short stature inhabit tropical rain forest environments. This is particularly true of the New Guinea small-bodied populations in the area of Mount Goliath, who are smaller than their neighbors in the lowland tropical rain forests (Diamond, 1992). The Kalahari San and the Andean and Nepalese highlanders, though normally not designated as "pygmies" but still quite small in average height and weight, also do not inhabit rain forest environments. This suggests that we should at least entertain the possibility that pygmies are as small as they are for other reasons, either in addition to, or instead of, the traditional climatic adaptation hypotheses. In the larger literature on mammalian physiological ecology, a number of authors (e.g., McNab, 1971; Scho-

⁸Readers should be cautioned not to misinterpret this residual as if it were a regression size-adjusted value. Also, the fact that it is a negative residual from a trend of negative correlation cannot be taken as "extra-strong" evidence for the climatic explanation, unless we wish to assume that there are no other potential factors yielding size decrease in the pygmies or other groups. We know that such an assumption is untenable.

lander, 1956) have suggested explanations for patterns of body size variation which are complementary or alternatives to the traditional climatic models (see below).

Experimental studies and simulations. The strongest test of thermoregulatory adaptations in the pygmies or any other group is direct experimental investigation of predicted physiological responses, rather than comparative and correlative studies of morphologies and climatic variables. In Arnold's (1983) framework, this is essentially testing whether significant relationships hold between patterns of variation in relevant morphological features and certain highly specific performance tasks, such as the ability to maintain adequate body temperatures during heat stress tests or when hunting in rain forest conditions (the subsequent step in this procedure is to determine whether the variation in performance actually relates to evolutionary fitness in natural habitats). It is surprising, in light of the widespread acceptance of heat adaptation scenarios of pygmy size and morphology, that no extensive and rigorously controlled investigations of the thermoregulatory physiology of pygmies compared to nonpygmies have been undertaken. Nevertheless, there are a few relevant empirical and theoretical studies.

Field studies which have attempted to test for physiological advantages to the pygmy morphotype include Pagezy (1978) and Ghesquiere and Karvonen (1981), both of which focused on the pygmoid Twa and Oto villagers in the Lake Tumba region of Zaire. Pagezy's (1978) study of women demonstrated mean differences in adult proportions between the Twa and Oto, and she concluded (pp. 683–687) that, in addition to smaller overall size, the "relative lengths of the lower limbs, compared to height, is shorter in the Twa women's group, as is their weight/body surface ratio. These two ratios lead us to suppose that Twa women have made a better morphological adaptation to heat tolerance in the hot and wet climate." However, her comparison of maximal strength (right and left handgrip), three rest tests (vital capacity, blood hemoglobin concentration, resting heart rate), and a test of

strenuous work (estimation of aerobic capacity and working capacity through submaximal tests) revealed no advantages in the smaller Twa. Pagezy (1978) stressed that her results were preliminary and potentially clouded by uncontrolled scaling effects, however.

Ghesquiere and Karvonen (1981) took anthropometric data on 25 adult male Twa pygmies and then determined the response of 15 of the men to graded exercise on a bicycle ergometer. Physiological variables examined include lung measurements (forced vital capacity, one-second forced expiratory volume, lung ventilation), heart rate, respiratory frequency, systolic and diastolic blood pressure, and hand grip forces. Once again, the sample of pygmies demonstrated no superiority in these performance criteria. Results of the above two studies must be considered equivocal, however, since the comparisons could not be performed under carefully controlled experimental conditions and sampling procedures, despite every effort by the investigators to combat very difficult field conditions.

Austin and Ghesquiere (1976) compared samples of Bantu Ntomba and pygmy Twa men in a heat acclimatization test and a test of tolerance to humid heat stress. These involved walking at 5 km/hr in the afternoon sun and exposure to heat by means of a hot water bath. In both of these tests of heat tolerance, the pygmies appeared to be more stressed in terms of body core temperature and heart rate. In explaining their results, Austin and Ghesquiere (1976) invoke a theoretical consideration which directly undermines many of the assumptions in the weight/surface area/climate models. They suggest that the higher surface area-to-weight ratios associated with the small size of the pygmies may in fact be a disadvantage in high heat stress environments, allowing for high heat gains through radiation and convection. This is supported by a study on obese and lean women by Bar-Or et al. (1969), which demonstrated that under the most stressful heat conditions, lean subjects had higher heat storage rates than obese subjects (though this pattern was reversed in more moderate conditions). Bar-Or et al. (1969) suggest that when the ambient tem-

perature is much higher than skin temperature, a high surface area-to-weight ratio may be disadvantageous. Such conditions are not characteristic of the rain forest environment, however, and this limits the applicability of these theoretical considerations to scenarios of heat adaptation in African pygmies. In addition, Austin and Ghesquiere's (1976) results have to be viewed skeptically, since these experiments were carried out under difficult conditions and are necessarily preliminary. Additionally, the tests were performed in the open under direct exposure to the sun, and not in the closed, environment of the forest where pygmies spend much of their time. Other controlled experimental studies by Strydom and Wyndham (1963) and Shvartz et al. (1973) failed to reveal any physiological advantages to particular morphologies and surface area-to-weight values.

A subsequent computer simulation by Austin and Lansing (1986) suggested that while a weak but consistent positive relationship between surface area-to-weight ratio and heat tolerance could be demonstrated for most conditions of heat stress, under extremely hot, humid conditions (40–50°C, 80% relative humidity), this relationship becomes negative. Their model further indicates that in high heat stress situations, where radiation and convection heat exchange is reversed from environment to organism, the primary avenue of heat loss is via evaporation. Their results show the greatest difference in thermophysiological measurements between small and normal phenotypes is in open area simulations, suggesting a greater potential for thermophysiological selection of high surface area-to-weight ratios in savanna, steppe, and desert areas as compared to tropical rain forests, with their combination of high ambient temperatures, extremely high relative humidity, and low levels of air movement. Once again, however, it needs to be stressed that the temperature and humidity values utilized in their high-heat simulated environment are different from those normally seen in the rain forest. Additionally, most of the above studies directly address hypotheses of size decrease based on higher surface area to volume relationships, rather than reduced in-

ternal heat production (cf. Cavalli-Sforza, 1986).

In a careful review of these and other physiological studies of climatic adaptation, Ruff (1994) raises many relevant issues regarding inadequacies of experimental design and execution which require that we treat all these conclusions as very preliminary. We agree, but also stress that such data provide the only experimental results that we have of what otherwise must remain by definition completely untested assumptions in the comparative studies. We also reiterate that even a complete rejection of the thermoregulatory hypothesis as it applies to pygmy microevolution, a position which we would not advocate at this time, obviously does not require a similar rejection of the more general association and its physiological basis across other human groups. We agree with most other authorities in suggesting that the heat-adaptation hypothesis of size reduction in pygmies is a very reasonable hypothesis which simply requires additional experimental testing.

In noting the obvious incongruence presented by their experimental results and the fact that the world's smallest humans often reside in very hot and humid tropical rain forest environments, Austin and Lansing (1986, p. 166) concluded that "perhaps this argues for something other than thermoregulatory selection to explain pygmies and pygmoids in tropical areas." We turn now to one such alternative adaptive explanation for the reduced overall size of pygmy groups.

Food resources and body size

Many discussions of the adaptive bases of small body size in African pygmies and other short-statured groups offer multiple scenarios for the observed pattern. Alternatives and/or additions to selection for thermoregulatory efficiency include selection for decreased caloric needs, and selection for reduced cost of mobility in the dense understory of the tropical rain forest (e.g., Cavalli-Sforza, 1986; Omoto, 1989; Diamond, 1992). We will not consider the mobility hypothesis, since it is not mutually exclusive from the thermoregulatory-efficiency hypothesis.

The argument that pygmy groups may have undergone strong selection for micro-evolutionary size reduction in order to yield reduced caloric needs in the face of limited food availability in the tropical rain forest has also not been subjected to direct testing. There are several pieces of indirect evidence that are consistent with this hypothesis, however. Bailey (1991a) has shown that Efe are smaller than neighboring horticulturalists and other Africans throughout postnatal development, indicating reduced caloric needs from an early age. Bailey et al. (1989), Headland (1987), and Bailey and Headland (1991) have suggested that the tropical rain forest offers a very limited supply of calories, particularly in the form of carbohydrates and fat, for human foragers. The Efe, reported here, obtain approximately two thirds of their calories in the form of crop plants cultivated by neighboring Lese villagers (Bailey and Peacock, 1988), and no African pygmy group subsists in the forest independently of cultivated foods for more than several weeks (Bahuchet and Guillaume, 1982; Bailey, 1991b; Bailey et al., 1989). Bailey et al. (1989, p. 62) conclude that "resources in undisturbed tropical rain forests may be so poor, variable, and dispersed that they cannot support viable populations of hunters and gatherers," and further (p. 73) that it is "very possible that human adaptability did not include the capacity to subsist for long periods of time in tropical forests until the development of ways to alter the density and distribution of edible resources through domestication of plants and clearing of climax forest." This argument suggests that certain food resources might be quite limited in this environment, thus exerting selection for decreased size. In birds, Price and Grant (1984) have demonstrated that smaller juveniles experience a selective advantage relative to their larger conspecifics, due to reduced energetic requirements. This difference would presumably be particularly important during times of general food shortage.

Cavalli-Sforza (1986) has depicted the African forest as isolated or "insular," and invoked ecological explanations accounting for body size change in populations of mammals inhabiting islands (e.g., Heaney, 1978). The

general "island rule" in mammals holds that large mammals generally evolve toward smaller body size on islands, while small mammals tend to get larger (Thaler, 1973; Foster, 1964; Van Valen, 1973; Sondaar, 1977). The ecological basis of such size shifts is generally thought to involve increased competition over limited food resources. It is well recognized that numerous other mammals in addition to *Homo sapiens* have dwarfed populations, subspecies, or species varieties in the tropical rain forest zone (Jeffreys, 1951). In our closest living relatives, the chimpanzees, we also see a diminution in overall size in the species (*Pan paniscus*) most restricted to the tropical rain forest environment.⁹

A final point to make regarding the limited-resource hypothesis is that it indirectly weakens the thermoregulatory hypothesis by raising the very real possibility that the various groups of pygmies now living in tropical rain forests did not necessarily evolve there, and therefore they could not have been subjected to the long-term, strong selection thought to be associated with rain forest climates (Diamond, 1992). Additional ethnographic, archeological, and biological data are needed to more fully examine this hypothesis.

An alternative perspective to the limited-resource hypothesis relates to the effects of seasonality on optimal body sizes. Boyce (1978, 1979; Lindstedt and Boyce, 1985) and other ecologists have suggested that large size should be favored in seasonal environments where food shortages occur or food is temporarily unavailable. This is due to the fact that even though larger individuals require more food, they can survive longer

⁹It has become commonplace to argue that the name "pygmy chimpanzee" is a misnomer, and that this species is not smaller than the "common" chimpanzee, *Pan troglodytes*. This confuses the statistical parameters of mean and range. Just as with the case of human pygmies relative to nonpygmies, *P. paniscus* is significantly smaller on average than the total mean for *P. troglodytes* (Shea, 1984; Leigh, 1992). However, of course there is very considerable overlap between the size ranges in the two groups. In fact, the pygmy chimpanzees may not be significantly smaller in average weight than the eastern variant of common chimpanzee, *Pan troglodytes schweinfurthii* (Jungers and Susman, 1984), whereas they are smaller than *Pan troglodytes troglodytes*, and we cannot be certain at this point about *Pan troglodytes verus* (Jungers and Susman, 1984; Shea, 1984).

without food than can smaller individuals. Murphy (1985) supports a similar argument as regards variation in body size in house sparrows and other bird species. Obviously, a corollary of this argument is that smaller size should be selectively advantageous in more stable environments, where selective intensities are milder but relatively constant (Murphy, 1985). The tropical rain forest environment of the pygmies should be one of a relatively constant but fairly low level of resource availability, and therefore such factors should be considered alongside the climatic models in accounting for reduced size in these humans, whether such size decrease ultimately turns out to be genetic or ecophenotypic.

CONCLUSIONS

Our results demonstrate that consideration of the adaptive basis of pygmy body proportions requires a careful analysis of patterns of growth allometry. We find that while adult Efe pygmies do indeed exhibit significantly different body proportions than adults of other African groups, these differences predominantly result from ontogenetic scaling, or the sharing of common patterns of growth allometry.

The implications of these findings for traditional views of the microevolution of African pygmies are considerable. A pattern of allometric truncation (ontogenetic scaling) accords with data from various other experimental and natural models of size change resulting from altered levels of GH and IGF-1 (Shea, 1988, 1990, 1992). Our increasing understanding of the hormonal control of complex allometric trajectories suggests that previous assessments (e.g., Vallois and Marquer, 1976; Marquer, 1972) characterizing pygmies as markedly divergent and "archaic" in their body and skeletal morphology have simply failed to appreciate the ways in which a basic shift in body size can ramify along multiple allometric pathways to yield a seemingly quite different terminal morphology. We find no evidence in this comparative allometric investigation to support arguments that pygmies are particularly distinctive or primitive in their morphology in relation to other groups of modern hu-

mans. This conclusion is supported by studies of other short-statured groups currently underway (e.g., Shea and Pagezy, 1988; Shea et al., 1992).

This investigation also suggests that the correlation between specific body proportions and climate noted in some previous studies (e.g., Hiernaux, 1968, 1977) simply reflects the allometric consequences of changes in overall body size. This focus on the morphological correlates of size change leads us to review previous arguments concerning the potential adaptive nature of the overall size decrease itself in African pygmies and other such groups around the world. We conclude that hypotheses of heat adaptation and limited food resources are both reasonable, but largely untested. Future work should be directed at developing controlled tests of these hypotheses where possible. In considering these selective hypotheses, we should also not rule out a priori the possibility that size change (and correlated allometric consequences) in some or all of these human groups has occurred through genetic drift or other nonadaptive processes.

ACKNOWLEDGMENTS

B.T.S. thanks the National Science Foundation (BNS-8519548) and Northwestern University for financial support. Sandra Inouye provided helpful assistance and discussion with data analysis, and Bill Jungers kindly shared his program for bivariate RMA comparisons. R.C.B. acknowledges the National Science Foundation (BNS-8617832) and the Swan Fund for their financial support of his field research. We are especially grateful to Robert Aunger, who assisted with the anthropometry, and the Efe men, women, and children who participated in the study.

LITERATURE CITED

- Albrecht GH (1978) The craniofacial morphology of the Sulawesi macaques: Multivariate approaches to biological problems. *Contrib. Primatol.* 13:1-151.
- Arnold SJ (1983) Morphology, performance and fitness. *Am. Zool.* 23:347-361.
- Atchley WR, and Hall BK (1991) A model for development and evolution of complex morphological structures. *Biol. Rev.* 66:101-157.
- Austin DM, and Ghesquiere J (1976) Heat tolerance of

- Bantu and Pygmoid groups of the Zaire River Basin. *Hum. Biol.* 48:439-453.
- Austin DM, and Lansing MW (1986) Body size and heat tolerance: A computer simulation. *Hum. Biol.* 58:153-169.
- Bahuchet S, and Guillaume H (1982) Aka-farmer relations in the northwest Congo basin. In E Leacock and R Lee (eds.): *Politics and History in Band Societies*. Cambridge: Cambridge University Press, pp. 189-211.
- Bailey RC (1991a) The comparative growth of Efe pygmies and African farmers from birth to age 5 years. *Ann. Hum. Biol.* 18:113-120.
- Bailey RC (1991b) The Behavioral Ecology of Efe Pygmy Men in the Ituri Forest, Zaire. Ann Arbor: Museum of Anthropology, University of Michigan.
- Bailey RC, and DeVore I (1989) Research on the Efe and Lese populations of the Ituri Forest, Zaire. *Am. J. Phys. Anthropol.* 78:459-472.
- Bailey RC, and Headland T (1991) The tropical rain forest: Is it a productive habitat for human foragers? *Hum. Ecol.* 19:261-285.
- Bailey RC, and Peacock NR (1988) Efe pygmies of Northeast Zaire: Subsistence strategies in the Ituri Forest. In I de Garine and GA Harrison (eds.): *Coping With Uncertainty in Food Supply*. Oxford: Clarendon Press, pp. 88-117.
- Bailey RC, Head G, Jenike M, Owen B, Rechtman R, and Zechenter E (1989) Hunting and gathering in tropical rain forest: Is it possible? *Am. Anthropol.* 91:59-82.
- Bailey RC, Jenike MR, Ellison PT, Bentley GR, Harrigan AM, and Peacock NR (1992) The ecology of birth seasonality among agriculturalists in central Africa. *J. Biosoc. Sci.* 24:393-412.
- Bakonyi M (1976) Contribution a l'Étude du Squelette des Pygmées (Ba)Mbuti de l'Ituri (Zaire). Geneva: Université de Geneve.
- Bar-Or O, Lundergren MH, and Buskirk ER (1969) Heat tolerance in exercising and obese women. *J. Appl. Physiol.* 26:403-409.
- Baum DA, and Larson A (1991) Adaptation reviewed: A phylogenetic methodology for studying character macroevolution. *Syst. Zool.* 40:1-18.
- Baumann G, Shaw MA, and Merimee TJ (1989) Low levels of high-affinity growth hormone-binding protein in African pygmies. *N. Engl. J. Med.* 320:1705-1709.
- Bowcock A, and Sartorelli V (1990) Polymorphism and mapping of the IGF1 gene, and absence of association with stature among African pygmies. *Hum. Genet.* 85:349-354.
- Boyce MS (1978) Climatic variability and body size variation in the muskrats (*Ondatra zibethicus*) of North America. *Oecologia* 36:1-20.
- Boyce MS (1979) Seasonality and patterns of natural selection for life histories. *Am. Nature* 114:569-583.
- Boyd WC (1963) Four achievements of the genetical method in physical anthropology. *Am. Anthropol.* 65:243-252.
- Bryant PJ, and Simpson P (1984) Intrinsic and extrinsic control of growth in developing organs. *Quart. Rev. Biol.* 59:387-415.
- Cameron N (1986) The methods of auxological anthropometry. In F Falkner and JM Tanner (eds.): *Human Growth: A Comprehensive Treatise*, 2nd ed. Vol 3: Methodology; Ecological, Genetic, and Nutritional Effects on Growth. New York: Plenum Press, pp. 3-46.
- Cavalli-Sforza LL (ed.) (1986) *African Pygmies*. Orlando: Academic Press.
- Cheverud JM (1982) Relationships among ontogenetic, static, and evolutionary allometry. *Am. J. Phys. Anthropol.* 58:1-11.
- Cheverud JM (1988) A comparison of genetic and phenotypic correlations. *Evolution* 42:958-968.
- Clarke MRB (1980) The reduced major axis of a bivariate sample. *Biometrics* 67:441-446.
- Cock AG (1966) Genetical aspects of metrical growth and form in animals. *Q. Rev. Biol.* 41:131-190.
- Crognier E (1981) Climate and anthropometric variations in Europe and the Mediterranean area. *Annals Hum. Biol.* 8:99-107.
- Czekanowski J (1922) *Forschungen im Nil-Kongo-Zwischengebiet. Anthropologische Beobachtungen. Wissenschaftliche ergebnisse der Deutschen Zentral-Afrika-Expedition 1907-1908. Ethnographie-Anthropologie IV*. Leipzig: Klinkhardt and Biermann.
- DeBeer GR (1940) *Embryos and Ancestors*. Oxford: Clarendon Press.
- Diamond J (1992) A question of size. *Discover Magazine* (May), pp. 70-77.
- Dietz WH, Marino B, Peacock NR, and Bailey RC (1989) Nutritional status of Efe pygmies and Lese horticulturalists. *Am. J. Phys. Anthropol.* 78:509-518.
- Ellison PT, Peacock NR, and Lager C (1989) Ecology and ovarian function among Lese women of the Ituri Forest, Zaire. *Am. J. Phys. Anthropol.* 78:519-526.
- Foster JB (1964) Evolution of mammals on islands. *Nature* 202:234-235.
- Frazzetta TH (1975) *Complex Adaptations in Evolving Populations*. Sunderland, MA: Sinauer Associates.
- Froesch ER, Schmid C, Schwander J, and Zapf J (1985) Actions of insulin-like growth factors. *Annu. Rev. Physiol.* 47:443-467.
- Gates RR (1958) The African pygmies. *Acta Genet. Med. Gemell.* 12:159-212.
- Gates RR (1961) The Melanesian dwarf tribe of Aiome, New Guinea. *Acta Genet. Med. Gemell.* 10:277-311.
- Geffner ME, Bailey RC, Bersch N, Vera JC, and Golde DW (1993) Insulin-like growth factor-I unresponsiveness in an Efe pygmy. *Biochem. Biophys. Res. Commun.* 193:1216-1223.
- Geffner ME, Bailey RC, Bersch N, Cortez AB, and Golde DW (1994) In vitro IGF-I resistance in 5 Efe pygmies. *J. Pediatr. Res.* (in press).
- Ghesquiere JL, and Karvonen MJ (1981) Some anthropometric and functional dimensions of the pygmy (Kivu Twa). *Ann. Hum. Biol.* 8:119-134.
- Gould SJ (1966) Allometry and size in ontogeny and phylogeny. *Biol. Rev.* 41:587-640.
- Gould SJ (1975) Allometry in primates, with emphasis on scaling and the evolution of the brain. *Contrib. Primatol.* 5:244-292.
- Gould SJ (1977) *Ontogeny and Phylogeny*. Cambridge: Harvard University Press.
- Gould SJ (1989) A developmental constraint in *Cerion*, with comments on the definition and interpretation of constraint in evolution. *Evolution* 43:516-539.
- Gould SJ (1992) Constraint and the square snail: Life

- at the limits of a covariance set. The normal teratology of *Cerion disforme*. Biol. J. Linn. Soc. 47:407-437.
- Gould SJ, and Lewontin RC (1979) The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. Proc. R. Soc. Lond. [Biol.] 205:581-598.
- Gould SJ, and Vrba ES (1982) Exaptation—A missing term in the science of form. Paleobiology 8:4-15.
- Gusinde M (1948) Urwaldmenschen am Ituri. Anthropologisch-biologische Forschungsergebnisse bei Pygmaen und Negeren im ostlichen Belgisch-Kongo a.d.J. 1934/35. Vienna: Springer-Verlag.
- Gusinde M (1955) Pygmies and pygmoids: Twides of tropical Africa. Anthropol. Q. 28:3-61.
- Hanna JM, Little MA, and Austin DM (1989) Climatic physiology. In MA Little and JD Haas (eds.): Human Population Biology. New York: Oxford University Press, pp. 132-151.
- Headland TN (1987) The wild yam question: How well could independent hunter-gatherers live in a tropical rainforest environment? Hum. Ecol. 15:463-491.
- Heaney LR (1978) Island area and body size of insular mammals: Evidence from the tri-colored squirrel (*Callosciurus prevosti*) of Southeast Asia. Evolution 32:29-44.
- Hiernaux J (1968) La diversité humaine en Afrique subsaharienne. Recherches biologiques. Bruxelles: Institut de Sociologie de l'Université Libre de Bruxelles.
- Hiernaux J (1974) The People of Africa. London: Weidenfeld and Nicolson.
- Hiernaux J (1977) Long-term biological effects of human migration from the African savanna to the equatorial forest: A case study of human adaptation to a hot and wet climate. In GA Harrison (ed.): Population Structure and Human Variation. Cambridge: Cambridge University Press, pp. 187-218.
- Hiernaux J, and Froment A (1976) The correlations between anthropobiological and climatic variables in sub-Saharan Africa: revised estimates. Hum. Biol. 48:757-767.
- Hiernaux J, Rudan P, and Brambati A (1975) Climate and the weight/height relationship in sub-Saharan Africa. Ann. Hum. Biol. 2:3-12.
- Hooper ACB (1977) A further study of the effects of selection for relative bone length. J. Anat. 121:495-496.
- Howells WW (1944) Mankind So Far. Garden City, NY: Doubleday.
- Huxley JS (1932) Problems of Relative Growth. London: MacVeagh.
- Jeffreys MDW (1951) Pygmies—human and otherwise. S. Afr. J. Sci. 47:227-233.
- Jungers WL (1982) Lucy's limbs: Skeletal allometry and locomotion in *Australopithecus afarensis*. Nature 297:676-678.
- Jungers WL, and Stern JT Jr (1983) Body proportions, skeletal allometry and locomotion in the Hadar hominids: A reply to Wolpoff. J. Hum. Evol. 12:673-684.
- Jungers WL, and Susman RL (1984) Body size and skeletal allometry in African apes. In RL Susman (ed.): The Pygmy Chimpanzee: Evolutionary Biology and Behavior. New York: Plenum Press, pp. 131-177.
- Katz MJ (1980) Allometry formula: A cellular model. Growth 44:89-96.
- Kollman J (1905) Neue Gedanken über das alte Problem von der Abstammung des Menschen. Corresp.-Bl. Deutsch. Ges. Anthropol. Ethnol. Urges. 36:9-20.
- Lande R (1979) Quantitative genetic analysis of multivariate evolution, applied to brain: Body size allometry. Evolution 33:402-416.
- Lande R, and Arnold SJ (1983) The measurement of selection on correlated characters. Evolution 37:1210-1226.
- Leigh SL (1992) The Ontogeny of Body Size Dimorphism in Anthropoid Primates. PhD dissertation. Northwestern University, Evanston, Illinois.
- Leof EB, Wharton W, Van Wyk JJ, and Pledger WJ (1982) Epidermal growth factor and somatomedin C regulate G₁ progression in competent BALB/c-3T3 cells. Exp. Cell Res. 141:107-115.
- Lewin R (1991) A hip theory for human evolution. New Scientist 16:20.
- Lindstedt SL, and Boyce MS (1985) Seasonality, fasting endurance and body size in mammals. Am. Nat. 125:873-878.
- Marquer P (1972) Nouvelle contribution à l'étude du squelette des pygmées occidentaux du centre Africain comparé à celui des pygmées orientaux. Mem. Nat. Hist. A 72:1-122.
- Martin R (1914) Lehrbuch der Anthropologie. Jena: Fischer.
- McKinney ML (ed.) (1988) Heterochrony in Evolution: A Multidisciplinary Approach. New York: Plenum Press.
- McKinney ML, and McNamara KJ (1990) Heterochrony: The Evolution of Ontogeny. New York: Plenum Press.
- McNab BK (1971) On the ecological significance of Bergmann's Rule. Ecology 52:845-854.
- Merimee TJ, Rimoin DL, Rabinowitz D, and Cavalli-Sforza LL (1968) Metabolic studies in the African pygmy. Trans. Assoc. Am. Physicians 81:221-231.
- Merimee TJ, Zapf J, Hewlett B, and Cavalli-Sforza LL (1987) Insulin-like growth factors in pygmies. N. Engl. J. Med. 15:906-911.
- Merimee TJ, Baumann G, and Daughaday W (1990) Growth hormone-binding protein: II. Studies in pygmies and normal statured subjects. J. Clin. Endocrinol. Metab. 71:1183-1188.
- Merimee TJ, Hewlett B, Wood W, Bowcock A, and Cavalli-Sforza LL (1989) The GH receptor gene in the African pygmy. Trans. Assoc. Am. Physicians 120:163-169.
- Murphy EC (1985) Bergmann's rule, seasonality, and geographic variation in body size of house sparrows. Evolution 39:1327-1334.
- Oberbauer AM, Currier TA, Nancarrow CD, Ward KA, and Murray JD (1992) Linear bone growth of oMT1a-oGH transgenic male mice. Am. J. Physiol. 262:E936-E942.
- Omoto K (1984) The Negritos: Genetic origins and microevolution. Acta Anthropogenet. 8:137-147.
- Omoto K (1989) Genetic studies of human populations in Asian-Pacific area with special reference to the origins of the Negritos. In H Obha, I Hayami, and K Mochizuki (eds.): Current Aspects of Biogeography in West Pacific and East Asian Regions. Tokyo: The University Museum, Nature and Culture, No. 1, pp. 135-146.
- Pagezy H (1978) Morphological, physical and ethoecolog-

- ical adaptations of Oto and Twa women living in the equatorial forest (Tumba Lake, Zaire). *J. Hum. Evol.* 7:683–692.
- Plotnick RE (1989) Application of bootstrap methods to reduced major axis line fitting. *Syst. Zool.* 38:144–153.
- Price TD, and Grant PR (1984) Life history traits and natural selection for small body size in a population of Darwin's finches. *Evolution* 38:483–494.
- Raff RA, and Kaufman TC (1983) *Embryos, Genes and Evolution*. Bloomington: Indiana University Press.
- Rayner JMV (1975) Linear relations in biomechanics: The statistics of scaling functions. *J. Zool. Lond.* 206:415–439.
- Rechler MM, Nissley SP, and Roth J (1987) Hormonal regulation of human growth. *N. Engl. J. Med.* 316: 941–942.
- Ricker WE (1973) Linear regressions in fishery research. *J. Fish. Res. Board Can.* 30:409–434.
- Riedel R (1978) *Order in Living Organisms*. New York: John Wiley and Sons.
- Rimoin DL, and Horton WA (1978) Short stature. Part I. *J. Pediatr.* 92:523–528.
- Roberts DF (1953) Body weight, race and climate. *Am. J. Phys. Anthropol.* 11:533–558.
- Roberts DF (1978) *Climate and Human Variability*, 2nd ed. Menlo Park: Cummings Publishing Co.
- Romer AS (1959) *The Vertebrate Story* (4th ed. of "Man and the Vertebrates"). Chicago: University of Chicago Press.
- Ruff CB (1991) Climate and body shape in hominid evolution. *J. Hum. Evol.* 21:81–106.
- Ruff CB (1993) Climatic adaptation and hominid evolution: The thermoregulatory imperative. *Evol. Anthropol.* 2:53–59.
- Ruff CB (1994) Morphological adaptation to climate in modern and fossil hominids. *Yrbk. Phys. Anthropol.* 37:65–108.
- Schebesta P (1938) *Die Bambuti-Pygmaen vom Ituri. I.—Geschichte, Geographie, Umwelt, Demographie und Anthropologie der Ituri-Bambuti, belgisch Congo*. Bruxelles: G. van Campenhout.
- Schebesta P (1952) *Les pygmées du Congo Belge*. Mem. Inst. Roy. Colonial Belge, Sciences Morales et Politiques, Collection in 8°, 26(2).
- Scholander FP (1956) Climatic rules. *Evolution* 10: 339–340.
- Schreider E (1950) Geographic distribution of the body weight/body surface ratio. *Nature* 165:286.
- Schultz AH (1930) The skeleton of the trunk and limbs of higher primates. *Hum. Biol.* 2:303–438.
- Shea BT (1981) Relative growth of the limbs and trunk in the African apes. *Am. J. Phys. Anthropol.* 56:179–202.
- Shea BT (1983a) Phyletic size change and brain/body scaling: A consideration based on the African pongids and other primates. *Int. J. Primatol.* 4:33–62.
- Shea BT (1983b) Allometry and heterochrony in the African apes. *Am. J. Phys. Anthropol.* 62:275–289.
- Shea BT (1984) An allometric perspective on the morphological and evolutionary relationships between pygmy (*Pan paniscus*) and common (*Pan troglodytes*) chimpanzees. In RL Susman (ed.): *The Pygmy Chimpanzee: Evolutionary Biology and Behavior*. New York: Plenum Press, pp. 89–130.
- Shea BT (1985a) Bivariate and multivariate growth allometry: Statistical and biological considerations. *J. Zool. Lond.* 206:367–390.
- Shea BT (1985b) Ontogenetic allometry and scaling: A discussion based on growth and form of the skull in African apes. In WL Jungers (ed.): *Size and Scaling in Primate Biology*. New York: Plenum Press, pp. 175–206.
- Shea BT (1986) Scapula form and locomotion in chimpanzee evolution. *Am. J. Phys. Anthropol.* 70:475–488.
- Shea BT (1988) Heterochrony in primates. In ML McKinney (ed.): *Heterochrony in Evolution*. New York: Plenum Press, pp. 237–266.
- Shea BT (1989) Heterochrony in human evolution: The case for neoteny reconsidered. *Yrbk. Phys. Anthropol.* 32:69–101.
- Shea BT (1990) Dynamic morphology: Growth, life history, and ecology in primate evolution. In J de Rousseau (ed.): *Primate Life History and Evolution*. New York: Wiley-Liss, Inc., pp. 325–352.
- Shea BT (1992) A developmental perspective on size change and allometry in evolution. *Evol. Anthropol.* 1:125–134.
- Shea BT, and Pagezy H (1988) Allometric analyses of body form in Central African pygmies. *Am. J. Phys. Anthropol.* 75:269–270 (Abstract).
- Shea BT, Hammer RE, and Brinster RL (1987) Growth allometry of the organs in giant transgenic mice. *Endocrinology* 121:1924–1930.
- Shea BT, Hammer RE, Brinster RL, and Ravosa MJ (1990) Relative growth of the skull and postcranium in giant transgenic mice. *Genet. Res. Camb.* 56:21–34.
- Shea BT, Baumann G, Omoto K, and Misawa S (1992) Allometry and epigenetic control of size reduction in the Aeta pygmies of the Philippines. *Am. J. Phys. Anthropol. Suppl.* 14:150 (Abstract).
- Shvartz E, Saar E, and Benor D (1973) Physique and heat tolerance in hot dry and hot humid environments. *J. Appl. Physiol.* 34:799–803.
- Siddiqui RA, Blair HT, McCutcheon SN, Mackenzie DDS, Gluckman PD, and Breier BH (1990) Developmental patterns of plasma insulin-like growth factor-I (IGF-I) and body growth in mice from lines divergently selected on the basis of plasma IGF-I. *J. Endocrinol.* 124:151–158.
- Siddiqui RA, McCutcheon SN, Blair HT, Mackenzie DDS, Breier BH, and Gluckman PD (1992) Growth allometry of organs, muscles and bones in mice from lines divergently selected on the basis of plasma insulin-like growth factor-I. *Growth Dev Aging* 56:53–60.
- Simpson GG (1953) *The Major Features of Evolution*. New York: Columbia University Press.
- Sinervo B (1993) The effect of offspring size on physiology and life history. *Bioscience* 43:210–218.
- Sinervo B, Doughty P, Huey RB, and Zamudio K (1992) Allometric engineering: A causal analysis of natural selection on offspring size. *Science* 258:1927–1930.
- Sober E (1988) *Reconstructing the Past: Parsimony, Evolution and Inference*. Cambridge: MIT Press.
- Sondaar PY (1977) Insularity and its effect on mammal evolution. In MK Hecht, PC Goody, and BM Hecht (eds.): *Major Patterns of Vertebrate Evolution*. New York: Plenum Press, pp. 671–707.
- Strauss RE (1984) Allometry and functional feeding morphology in haplochromine cichlids. In AA Echelle

- and I Kornfield (eds.): *Evolution of Fish Species Flocks*. Orono: University of Maine Press, pp. 217–229.
- Strydom NB, and Wyndham CH (1963) Natural state of heat acclimatization of different ethnic groups. *Fed. Proc.* 22:801–808.
- Thaler L (1973) Nanisme et gigantisme insulaires. *La Recherche* 4:741–750.
- Thomson KS (1988) *Morphogenesis and Evolution*. New York: Oxford University Press.
- Trinkaus E (1981) Neanderthal limb proportions and cold adaptation. In CB Stringer (ed.): *Aspects of Human Evolution*. Symp. Soc. Study Hum. Biol. 21: 187–225.
- Tsutakawa RK, and Hewett JE (1977) Quick test for comparing two populations with bivariate data. *Biometrics* 33:215–219.
- Vallois HV (1927) L'omoplate des Négrilles et des Négritos. *Bull. Du Mus. Nat. Hist. Natur.* 33:333–335.
- Vallois HV (1940) New research on the western negrillos. *Am. J. Phys. Anthropol.* 26:449–471.
- Vallois HV, and Marquer P (1976) Les pygmées Baka du Cameroun: anthropologie et ethnographie avec une annexe démographique. *Mem. Mus. Nat. Hist. Natur. Serie A, Zoologie, Tome C*.
- Van Valen L (1973) Pattern and balance of nature. *Evol. Theory* 1:31–49.
- Vogl C, Atchley WR, Cowley DE, Crenshaw P, Murray JD, and Pomp D (1993) The epigenetic influence of growth hormone on skeletal development. *Growth Dev Aging* 57:163–182.
- Wilkerson L (1990a) SYSTAT: The System for Statistics. Evanston, IL: SYSTAT, Inc.
- Wilkerson L (1990b) SYGRAPH: The System for Graphics. Evanston, IL: SYSTAT, Inc.
- Wolf E, Rapp K, and Brem G (1991) Expression of metallothionein-human growth hormone fusion genes in transgenic mice results in disproportionate skeletal gigantism. *Growth Dev Aging* 55:117–127.
- Wolpoff MH (1983a) Lucy's lower limbs: Long enough for Lucy to be fully bipedal? *Nature* 304:59–61.
- Wolpoff MH (1983b) Lucy's little legs. *J. Hum. Evol.* 12:443–453.
- Zeng Z-B (1988) Long-term correlated response, interpopulation covariation, and interspecific allometry. *Evolution* 42:363–374.